GROWTH OF JUVENILE CHILKAT LAKE SOCKEYE SALMON IN RESPONSE TO DENSITY-DEPENDENT AND ENVIRONMENTAL FACTORS

By

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Abstract

Chilkat Lake, in northern Southeast Alaska, is home to a Sockeye Salmon *Oncorhynchus nerka* population that is an important component in local commercial, sport, and subsistence fisheries, and has been monitored since the late 1960s. The population began declining in the late 1980s, prompting fishery managers to evaluate the production potential of Chilkat Lake to determine if it could be a candidate for enhancement efforts such as fry stocking or lake fertilization. Sockeye Salmon fry were stocked into Chilkat Lake intermittently from 1989 to 2004 in both small- (< 50,000) and large-scale (2.6-5.3 million) events. The purpose of this study was to determine whether stocking of fry resulted in decreased freshwater growth due to density-dependent processes. Fish scales from the Alaska Department of Fish and Game's archived collection of adult Chilkat Lake Sockeye Salmon were measured and used as a proxy for fish growth. The objectives of this thesis were to 1) examine changes in juvenile Chilkat Lake Sockeye Salmon freshwater growth over time (1978-2012); 2) determine whether increased density of juvenile fry coupled with simultaneous climate events negatively affected freshwater growth of Chilkat Lake Sockeye Salmon; and 3) determine whether increased density of juvenile fry affected age at smoltification of Chilkat Lake Sockeye Salmon. We hypothesized that high fry density would slow growth and delay smoltification; however, these analyses produced variable results. We did not detect an effect of increased fry density on growth in the first year of fresh water, but found evidence for a subtle, negative relationship between fry density and second year freshwater growth of those fish that delayed migration. We also found that age at smoltification decreased with increasing fry density. Overall, the model results indicated that no factor or combination of factors related to stocking activity or climate consistently affected juvenile Sockeye Salmon scale growth, suggesting either unidentified, equally influential, or confounding mechanisms (e.g., high adult escapement and anomalous weather patterns).

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Chapter 1: General introduction

Pacific salmon (*Oncorhynchus* spp.) are an important biological, economic, and cultural resource for many Pacific Rim nations, such as the United States, Russia, and Japan (Brodeur et al. 2003). Pacific salmon hatch in freshwater lakes, rivers, and streams; spend most of their lives in the ocean; return to their natal environment to spawn; and die after spawning (Groot and Margolis 1991; Quinn 2005). Sockeye Salmon *O. nerka,* Chum Salmon *O. keta,* and Pink Salmon *O. gorbuscha* are the most abundant Pacific salmon (NPAFC 2002; Ruggerone et al. 2010; Ruggerone and Irvine 2018). Sockeye Salmon are found from the Sacramento River in California to the northern Bering Sea in Alaska and the Sea of Okhotsk in Russia (Burgner 1991). Most populations of Sockeye Salmon rear in lakes one to three years prior to emigrating to the ocean as smolts, but lake duration varies among systems (Groot and Margolis 1991; Quinn 2005). Growth is an important factor in determining time juvenile Sockeye Salmon spend in fresh water before undergoing smoltification and migrating to the ocean (Dickhoff et al. 1997), and faster growing individuals tend to migrate a year earlier than smaller individuals (Burgner 1991; Rich et al. 2009). Freshwater growth is affected by food availability, density dependence, and temperature (Foerster 1944; Koenings and Burkett 1987; Ruggerone and Rogers 2003; Reed et al. 2010).

Studies have shown that freshwater environments, such as lakes, are highly sensitive to climate variation (Adrian et al. 2009), and climate changes can potentially affect freshwater growth by changing the timing of spring breakup, altering the length of the growing season, and affecting food availability and a fish's ability to metabolize food (Winder and Schindler 2004; Schindler et al. 2005; Adrian et al. 2009; Griffiths and Schindler 2012; Griffiths et al. 2014). Under positive growing conditions (i.e., available food, moderate water temperature, and low intraspecific competition), juvenile Sockeye Salmon might grow sufficiently large to migrate to the ocean after one year (Quinn 2005). Smolt size tends to be strongly related to marine survival (Peterman 1984; Henderson and Cass 1991; Koenings et al. 1993) and can significantly influence recruitment (Ruggerone et al. 2013), indicating the importance of the freshwater juvenile stage in the life cycle of Sockeye Salmon. Climate indices, such as the Pacific Decadal Oscillation (PDO;

Mantua et al. 1997), have been shown to correlate with growth of juvenile sockeye salmon in freshwater environments (Rich et al. 2009; Griffiths et al. 2014).

In systems with low or declining Sockeye Salmon production created by limited available spawning habitat or prey availability, enhancement programs, such as hatchery stocking and lake fertilization, have increased the abundance of adult salmon returning to spawn (Hyatt and Stockner 1985; Koenings et al. 1989; Kyle et al. 1990). Systems considered to be spawning- or recruitment-limited are characterized by low fry density due to low adult escapement and/or limited available spawning habitat; these systems can potentially benefit from hatchery stocking (Koenings et al. 1989). Systems considered to be rearing area-limited have low production of natural forage available to Sockeye Salmon fry and/or unfavorable environmental conditions in the rearing environment; such systems might benefit from nutrient enrichment in the form of lake fertilization (Koenings et al. 1989). Hatchery stocking directly influences fry density; therefore, the effectiveness of stocking depends on a lake's capacity to sustain juvenile growth with increasing density. Previous and on-going Sockeye Salmon fry stocking programs have shown mixed results (Eggers et al. 2008; Habicht et al. 2013; Ackerman et al. 2015).

The Sockeye Salmon population in Chilkat Lake in Southeast Alaska has been monitored since the late 1960s because of its importance in local commercial, sport, and subsistence fisheries. Sockeye Salmon abundance declined in the early 1980s, rebounded briefly in the early 1990s, and then declined again in the mid-1990s, prompting fishery managers to evaluate the production potential of the lake. Although Chilkat Lake was initially thought to be nutrient-limited, limnological studies conducted by the Alaska Department of Fish and Game (ADF&G) Division of Fisheries Rehabilitation Enhancement and Development (FRED; Koenings and Burkett 1987; Barto 1996) concluded that the system was spawning habitat-limited, indicating the lake could support additional Sockeye Salmon fry (Eggers et al. 2008). Fry stocking, using eggs and milt collected from adult Chilkat Lake Sockeye Salmon and fertilized on-site, was conducted intermittently from 1989 to 2004 with modest numbers of fry (< 500,000) planted in on-site incubation boxes (small-scale) as well as large-scale stocking efforts in the mid-1990s and again in 2001. Large-scale fry stocking (2.6 – 5.3 million fry) involved conducting on-site egg takes and transporting the fertilized eggs to on off-site fish hatchery to overwinter and hatch before transporting the fry back to Chilkat Lake in early summer. In-season monitoring of outmigrating Sockeye Salmon smolts concluded that the increased fry density negatively impacted smolt size, as well as increased age at smoltification (Eggers et al. 2008; Duckett et al. 2010). As a result, all enhancement activities at Chilkat Lake were discontinued after 2004 (Duckett et al. 2010).

As part of the long-term monitoring of the Chilkat Lake Sockeye Salmon stock, adult fish scales with accompanying data including fish age, length, and sex have been compiled and archived for use by managers. Fish scales can be useful for determining the age of an individual fish, estimating overall growth and growth associated with years spent in both freshwater and marine environments, and determining stock of origin (Fukuwaka 1998). Studies have shown a linear correlation between scale radius and fish length as well as a positive correlation between body size and total number of circuli per scale during the years of freshwater growth for juvenile Sockeye Salmon (Fukuwaka and Kaeriyama 1997). ADF&G maintains archives of salmon scales used to provide age composition data to fishery managers, and measurements of these scales can be used to investigate ecological mechanisms, such as climate or density dependence, that might influence growth over time (e.g., Ruggerone and Rogers 2003; Ruggerone et al. 2007; Martinson et al. 2008; Agler et al. 2013; Griffiths et al. 2014). Scales from adult Sockeye Salmon have been collected at Chilkat Lake since the late 1960s, allowing an assessment of juvenile freshwater growth over time and the potential to detect responses to fry stocking in relationship to ecosystem and climate variability.

The goal of this study was to determine whether fry stocking resulted in decreased freshwater growth due to density-dependent processes. The timing of the Chilkat Lake fry stocking program overlapped with several years of high adult escapement and several strong climate events (Fig. 1.1). Based on the suspected density-dependent growth observed in outmigrating smolts during the years of fry stocking, we hypothesized that freshwater growth would decrease and age at smoltification would increase during years of high fry density. Our research objectives were to 1) examine changes in juvenile Chilkat Lake Sockeye Salmon freshwater growth over time (1978-2012); 2) determine whether increased density of juvenile fry coupled with simultaneous climate events negatively affected freshwater growth of Chilkat Lake Sockeye Salmon; and 3) determine whether increased density of juvenile fry affected age at smoltification of Chilkat Lake Sockeye Salmon.

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Figures

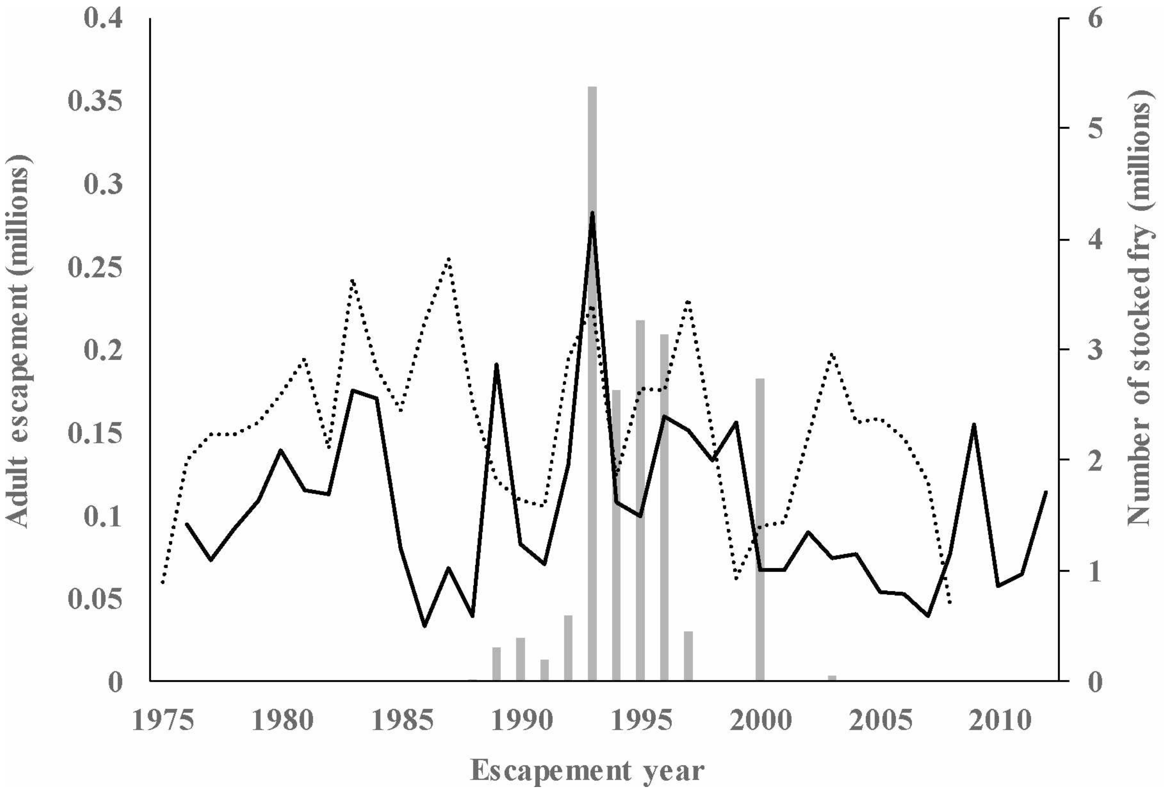

Figure 1.1. Total number of Sockeye Salmon fry stocked in Chilkat Lake (grey bars) in relation to adult Sockeye Salmon spawning escapement (black line) and the Pacific Decadal Oscillation (dotted line).

Chapter 2: Growth of juvenile Chilkat Lake Sockeye Salmon in response to density-dependent and environmental factors[1]

Abstract

Sockeye Salmon *Oncorhynchus nerka* populations in Chilkat Lake, Alaska have been monitored since the late 1960s. The population began declining in the late 1980s, prompting studies of the production potential of the lake. Chilkat Lake was supplemented with Sockeye Salmon fry intermittently during 1989–1998, 2001, and 2004 in both small- and large-scale events; however, in-season monitoring of outmigrating smolts suggested growth was negatively affected by increased fry density, so enhancement efforts were discontinued in 2004. The purpose of this study was to determine whether stocking of fry resulted in decreased freshwater growth due to density-dependent processes. Fish scales from adult Chilkat Lake Sockeye Salmon were measured and used as a proxy for fish growth. We hypothesized that high fry density would slow growth and delay smoltification but found variable support for this hypothesis. We did not detect an effect of increased fry density on growth in the first freshwater year, but growth in the second year of fresh water declined slightly with increasing fry density. Contrary to our hypothesis, age at smoltification tended to be younger in years with greater fry density. Ultimately, we did not identify a single factor or combination of factors that consistently affected juvenile Sockeye Salmon freshwater scale growth, suggesting that growth was due to other variables or the effect of the examined variables was masked by confounding mechanisms (e.g., increased fry density due to fry stocking and high adult escapement coinciding with strong climate events).

Introduction

Pacific salmon (*Oncorhynchus* spp.) are an important biological, economic, and cultural resource for many countries, such as the United States, Russia, and Japan (Brodeur et al. 2003). Sockeye Salmon *O. nerka,* Chum Salmon *O. keta,* and Pink Salmon *O. gorbuscha* are the most abundant Pacific salmon (NPAFC 2002; Ruggerone et al. 2010; Ruggerone and Irvine 2018). Sockeye

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[1] Neil, J. C., B. A. Agler, G. T. Ruggerone, M. D. Adkison, M. V. McPhee. Growth of juvenile Chilkat Lake Sockeye Salmon in response to density-dependent and environmental factors. Prepared for submission in Transactions of the American Fisheries Society.

Salmon are found from California to the northern Bering Sea in Alaska and the Sea of Okhotsk in Russia (Burgner 1991). Most populations of Sockeye Salmon rear in lakes one to three years prior to emigrating to the ocean (Groot and Margolis 1991). Abundance of juveniles in the freshwater environment can be limited by available spawning habitat and prey availability, sometimes prompting managers to employ strategies, such as hatchery stocking and lake fertilization, to increase the abundance of adult salmon returning to spawn (Hyatt and Stockner 1985; Koenings et al. 1989; Kyle et al. 1990).

Numerous studies document the density dependence of juvenile Sockeye Salmon growth (Foerster 1944; Koenings and Burkett 1987; Ruggerone and Rogers 2003). Growth is an important factor in determining residence time in fresh water prior to smoltification (Dickhoff et al. 1997), and faster growing individuals tend to migrate a year earlier than slower growing individuals (Burgner 1991; Rich et al. 2009; Tillotson et al. 2016). Freshwater growth is affected by food availability, density dependence, and temperature (Foerster 1944; Koenings and Burkett 1987; Ruggerone and Rogers 2003; Reed et al. 2010). Studies have shown that climate can affect freshwater growth by changing the timing of spring breakup and affecting food availability and an individual's ability to metabolize and process food (Winder and Schindler 2004; Schindler et al. 2005; Adrian et al. 2009; Griffiths and Schindler 2012; Griffiths et al. 2014). Under positive growing conditions (i.e., available food, warm water, and low intraspecific competition), juvenile Sockeye Salmon might grow sufficiently large to migrate to the ocean after one year (Quinn 2005). Smolt size tends to be strongly related to marine survival (Peterman 1984; Henderson and Cass 1991; Koenings et al. 1993) and can significantly influence recruitment (Ruggerone et al. 2013), indicating the importance of the freshwater juvenile stage in the life cycle of Sockeye Salmon.

Chilkat Lake, in Southeast Alaska, exemplifies the multifaceted relationship between fry abundance and lake rearing capacity. The Sockeye Salmon population has been monitored since the late 1960s. The population declined in the early 1980s, prompting fishery managers to evaluate Chilkat Lake as a potential candidate for lake enhancement efforts, such as fry stocking or lake fertilization (Eggers et al. 2008, 2010). Using a model developed by the Alaska Department of Fish and Game (ADF&G) Division of Fisheries Rehabilitation Enhancement and

Development (FRED), limnological evaluations of Chilkat Lake (Koenings and Burkett 1987; Barto 1996) concluded that the system was spawning habitat-limited rather than nutrient-limited, indicating the lake could support additional Sockeye Salmon fry (Eggers et al. 2008). Consequently, Chilkat Lake was subjected to variable and intermittent fry stocking from 1989 to 2004 (Eggers et al. 2008, 2010); however, in-season monitoring of outmigrating smolts during years of enhancement indicated a negative relationship between smolt size and increased fry density as well as an increase in age at smoltification, resulting in discontinuation of the stocking program after 2004 (Eggers et al. 2008; Duckett et al. 2010).

Retrospective analyses of fish scales present an opportunity to examine a population over many decades to see trends or patterns in growth. Studies have shown a linear correlation between scale radius and fish length as well as a positive correlation between body size and total number of circuli per scale during the years of freshwater growth for juvenile Sockeye Salmon (Fukuwaka and Kaeriyama 1997). ADF&G maintains archives of salmon scales used to provide age composition data to fishery managers. Measurements of these scales can be used to estimate growth in freshwater and marine environments (Fukuwaka and Kaeriyama 1997; Fukuwaka 1998), thus allowing investigation of ecological mechanisms, such as climate or density dependence, that might influence growth over time (e.g., Ruggerone and Rogers 2003; Ruggerone et al. 2007; Agler et al. 2013; Griffiths et al. 2014). Studies have used archived scale collections to evaluate growth and productivity and understand long-term effects on salmon populations (Martinson et al. 2008; Agler et al. 2013). Scales from adult Sockeye Salmon have been collected at Chilkat Lake since the late 1960s, allowing an assessment of juvenile freshwater growth over time and the potential to detect responses to fry stocking in relationship to ecosystem and climate variability.

The purpose of this study was to determine whether stocking of fry resulted in decreased freshwater growth due to density-dependent processes. Coincidentally, the timing of the Chilkat Lake fry stocking program overlapped with several years of high adult escapement and several strong climate events. Based on the suspected density-dependent growth observed in the outmigrating smolts during the years of fry stocking, we hypothesized that freshwater growth would decrease and age at smoltification would increase during years of high fry density. Our research objectives were to 1) examine changes in juvenile Chilkat Lake Sockeye Salmon freshwater growth over time (1978-2012); 2) determine whether increased density of juvenile fry coupled with simultaneous climate events negatively affected freshwater growth of Chilkat Lake Sockeye Salmon; and 3) determine whether increased density of juvenile fry affected age at smoltification of Chilkat Lake Sockeye Salmon.

Methods

Study area and stocking history

Chilkat Lake, located in northern Southeast Alaska approximately 48 km north of Haines, Alaska (Fig. 2.1), is home to Sockeye Salmon and Coho Salmon *O. kisutch*, Cutthroat Trout *O. clarkii*, Dolly Varden Char *Salvelinus malma*, Threespine Stickleback *Gasterosteus aculeatus*, and several species of sculpin *Cottus* spp. (ADF&G 1987). A clear lake with a maximum depth of 57 m and an average depth of 32.5 m (McPherson 1990), Chilkat Lake sustains one of the largest Sockeye Salmon runs in Southeast Alaska. Sockeye Salmon from Chilkat Lake, along with nearby Chilkoot Lake, support most of the Upper Lynn Canal drift gillnet fishery (Kelley and Bachman 1999; Heinl et al. 2011) and are an important component of the local subsistence fishery (Eggers et al. 2010). In response to decreasing adult escapement, Chilkat Lake was stocked with Sockeye Salmon fry intermittently from 1989-2004 with modest numbers (<500,000) planted in on-site incubation boxes (small-scale) as well as large-scale (2.6-5.3 million) stocking efforts in the mid-1990s and again in 2001 (Table 2.1).

Biological sampling

The Chilkat Lake Sockeye Salmon population has been monitored since the late 1960s, resulting in a long-term data set that includes escapement and biological data (age, sex, and fish length) as well as corresponding scales taken from adult Sockeye Salmon returning to the lake. Escapement estimates were derived from several different sources over the time series, including an adult weir at the mouth of Chilkat Lake from 1967-1995 and 1999-2007, mark-recapture studies from

1994-2007, and dual frequency identification sonar (DIDSON) at the mouth of Chilkat Lake beginning in 2008 (Eggers et al. 2010; Heinl et al. 2011).

Adult Sockeye Salmon return to Chilkat Lake from June through November. The population exhibits early and late run-timing modes (McPherson 1990) and is comprised of several different age classes. The dominant age classes are age 1.3 (European), fish that spend one winter in fresh water and three winters in the ocean, and age 2.3, fish that spend two winters in fresh water and three winters in the ocean. Age-1.3 fish return primarily from July to late August (early run), while age-2.3 fish return primarily from late August to mid-October (late run; McPherson 1990). Scales were collected from adults returning to Chilkat Lake between June and November beginning in 1967 at either the weir (1978-1995, 1999-2012) or on the spawning grounds (1996-1998). Accompanying biological data, including fish length and sex, were collected for most years. Scales were aged in-season by ADF&G personnel in Juneau, Alaska and the age and associated somatic data are housed in the ADF&G scale database.

Scale measurements

Scales were imaged and measured at the ADF&G Mark, Tag, and Age (MTA) Lab in Juneau. Following MTA protocols (Hagen et al. 2001), scales were selected based on specific criteria, including agreement with previous age designation, scale shape (indicating the scale was selected from the "preferred area," INFPFC 1963), clarity of growth pattern, visible last saltwater annulus, and sample date. Scales of age-1.3 fish included only those sampled between June 1 and August 20 of each year and age-2.3 between August 10 and November 15 to sample the peak of the run for each freshwater age. Some scales that did not meet all criteria were included in the data set to achieve an appropriate sample size (e.g., scales without a visible last saltwater annulus due to resorption or multiple scale pressings). These scales were retained only for analyses of earlier (i.e., fresh water) growth zones.

Our goal was to image and measure 50 scales from the dominant age classes (25 of each sex) per each return year whenever possible using the imaging software Screen Scan (Nanomach Anstalt © 2000). Images were stored as high-resolution digital files and measured using Image Pro Plus software (Media Cybernetics © 1993, 2009). Scales were measured from the focus to the outer edge of the last visible saltwater annulus using a perpendicular measurement axis drawn between the outer edges of the first saltwater annulus. All freshwater and saltwater annuli were identified as well as individual circuli within each annual growth zone (Fig. 2.2). The first freshwater growth zone (FW1, following the notation of Ruggerone and Rogers 2003) was measured from the focus to the outer edge of the last circulus of the FW1 annulus, and the second freshwater growth zone (FW2) for age-2.3 fish was measured from the end of the FW1 annulus to the outer edge of the last circulus of the FW2 annulus. Freshwater plus (FWPl), when present, was defined as growth immediately following the last freshwater annulus to the outer edge of the last circulus before the first saltwater circulus. Similarly, individual saltwater growth zones (SW1, SW2, and SW3) were measured from the end of the preceding annulus to the outer edge of the last circulus of the corresponding saltwater growth zone. Saltwater-plus (SWPl) growth was measured from the last saltwater annulus to the outermost edge of the scale. Specific measurements collected for each scale included total scale radius, distance between individual circuli, and total size of each individual growth zone (mm).

Analyses included measurements of the freshwater growth zones for the dominant age classes. Freshwater-plus growth was uncommon (age 1.3 = 9%, age 2.3 = 1%) and was not included in this assessment of freshwater growth because it presumably corresponded to growth in the estuary or early marine residence. All measures of total growth zone size (FW1 and FW2 individually) from each scale within a single year were averaged to create a single yearly growth measurement (Appendix A-1). Years with fewer than ten scale measurements were excluded from the final data set. We limited the time series to brood years (BY; the calendar year corresponding to the year of egg deposition) 1973-2006 to include data for years in which all year classes of the dominant age classes of Sockeye Salmon returned to Chilkat Lake as adults.

Statistical analyses

Between-sex differences in freshwater growth

Preliminary analyses were conducted to determine if freshwater growth differed between sexes. To test for differences between sexes within and across years among individual fish, we compared measurement data for both sexes for each freshwater growth zone (age-1.3 FW1, age-2.3 FW1, and age-2.3 FW2) using analysis of variance (ANOVA; R Core Team 2013). To account for variation across the target years and include between-year effects, a blocking model with interaction was considered:

$$FW_{ijk} = \alpha + \beta_1 Sex_i + \beta_2 BY_j + \gamma Sex_i BY_j + \varepsilon_{ijk} \qquad \text{Equation (2.1)}$$

where FW_{ijk} represented size of the freshwater growth zone for a given age class of fish k given sex i and brood year j, α represented mean size of the freshwater growth zone, $\beta_1 Sex_i$ represented overall difference between sexes, $\beta_2 BY_j$ represented differences in growth for the specified brood year, $\gamma Sex_i BY_j$ represented individual differences of a given sex among years to account for interaction, and ε_{ijk} represented residual error of fish k of sex i of brood year j.

Objective 1: Freshwater growth trends over time

Average size of each freshwater growth zone (FW1 and FW2) was calculated by brood year. To estimate average growth for all fish in the first year in fresh water for each brood year, regardless of age at smoltification (age-1 or age-2), we calculated FW1 for each brood year by weighting the average FW1 growth by the freshwater age composition of each brood year (represented as the proportion of age-1.3 and -2.3 adult Sockeye Salmon from each respective brood year calculated from the Chilkat Lake harvest and escapement brood table maintained by ADF&G; Steve Heinl, pers. comm.). For the purposes of these analyses, we refer to average FW1 growth as FW1.

FW1 and FW2 measurements were plotted over time (by brood year) and compared to average pre- and post-stocking growth to assess changes coinciding with fry stocking. Lack of harvest and escapement data (specifically for FW1) or insufficient scale samples for some years resulted in gaps in the time series for both growth zones examined (i.e., brood years 1973-1981, 1990-1994 for FW1 and 1974, 1979, 1990, 1992-1993 for FW2).

Objective 2: Density-dependent and climate effects on freshwater growth

We investigated density dependence by incorporating the total number of stocked fry ('Stocked'; small- and large-scale stocking values combined in years where both occurred) and adult spawning escapement ('Esc') as separate explanatory variables. To account for density-dependent effects of juvenile Sockeye Salmon remaining in the lake for an additional year, we also included the number of stocked fry in the previous year and adult escapement in the previous year as explanatory variables. Adult escapement estimates were provided by ADF&G (S. Heinl, pers. comm.). All density-dependent variables corresponded to the year in fresh water for each response variable (e.g., 1st year in fresh water for FW1 and 2nd year for FW2) and were normalized so that model coefficients could be directly compared.

To account for possible climate effects on freshwater growth, three environmental variables were considered as covariates: the Pacific Decadal Oscillation (PDO; data available at ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest), a recurring pattern of climate variability measured by sea surface temperature in the North Pacific Ocean (Mantua et al. 1997); the North Pacific Gyre Oscillation (NPGO; data available at http://www.o3d.org/npgo/npgo.php), a pattern of climate variability correlated with fluctuations of salinity and nutrients driven by ocean circulation (Di Lorenzo et al. 2008); and the El Niño–Southern Oscillation (ENSO), a pattern of climate variability that fluctuates every few years (Mysak 1986; Wolter and Timlin 1993; Huang et al. 2015). We included ENSO as a binary variable (1 for years categorized as having an El Niño winter and 0 for years without an El Niño winter; data available at http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) to account for possible nonlinear effects of ENSO events not captured by the continuous variation in sea surface temperature expressed by the PDO. The PDO and NPGO data were split into seasonal indices representing two distinct growing seasons: winter (November – March; indexed by calendar year in January) and spring/summer (April – July). The winter and spring/summer growing seasons represent key periods of freshwater growth for juvenile Sockeye Salmon because winter conditions set up conditions for spring/summer productivity, such as timing of spring thaw and zooplankton production crucial for juvenile Sockeye growth (e.g., Schindler et al. 2005).

We examined correlations among the following climate variables: winter PDO (WPDO), spring/summer PDO (SSPDO), winter NPGO (WNPGO), and spring/summer NPGO (SSNPGO); excluding variables with correlations of $r > 0.60$. After evaluating multicollinearity (Appendix A-2), WPDO, SSPDO, and WNPGO were retained in the full models, along with the binary ENSO variable. As with the density-dependent variables, all climate variables corresponded to the year in fresh water for each response variable, and all but the binary variable ENSO were normalized so that model coefficients could be directly compared.
The full models for among brood-year variation in freshwater growth zone size were:

$$FW1_j = \alpha + \beta_1 Stocked_j + \beta_2 Stocked_{j-1} + \beta_3 Esc_j + \beta_4 Esc_{j-1} + \beta_5 SSPDO_{j+1} + \beta_6 WPDO_{j+1} + \beta_7 WNPGO_{j+1} + \beta_8 ENSO_{j+1} + \varepsilon_{ij} \quad \text{Equation (2.2)}$$

$$FW2_j = \alpha + \beta_1 Stocked_j + \beta_2 Stocked_{j+1} + \beta_3 Esc_j + \beta_4 Esc_{j+1} + \beta_5 SSPDO_{j+2} + \beta_6 WPDO_{j+2} + \beta_7 WNPGO_{j+2} + \beta_8 ENSO_{j+2} + \varepsilon_j \quad \text{Equation (2.3)}$$

where FW_j represented average size of a given freshwater growth zone i (i.e., FW1 or FW2) for brood year j, and ε represented residual error for brood year j.

The relationships between freshwater growth and the density-dependent and environmental variables were examined and all possible combinations of explanatory variables for each individual response variable, including the null model, were compared using the Multi-Model Inference package in R (MuMIn; Bartón 2015). We restricted model comparisons only to those with negative density-dependent coefficients. The best model was selected according to lowest second-order corrected Akaike information criterion (AICc), which accounted for small sample size (Burnham and Anderson 2002). Model residuals for all candidate models (ΔAICc < 2) were plotted and examined for normality (Shapiro-Wilk test), temporal autocorrelation (autocorrelation function 'acf'), and influential outliers (Cook's distance).

Objective 3: Density-dependent effects on age at smoltification

The relationships between age at smoltification and the density-dependent and environmental variables were examined using a binary logistic regression model in R. Proportions of adult Sockeye Salmon from each brood year that smolted after one versus two years in fresh water (regardless of ocean age) were calculated using total return data (harvest and escapement) from the Chilkat Lake Sockeye Salmon brood table for 1979-2006. The full model was:

$$\ln(P_j/1\text{-}P_j) = \alpha + \beta_1 Stocked_j + \beta_2 Esc_j + \beta_3 SSPDO_j + \beta_4 WPDO_j + \beta_5 WNPGO_j + \beta_6 ENSO_j + \varepsilon_j \qquad \text{Equation (2.4)}$$

where P_j represented the proportion of adults from brood year j that smolted after two years in fresh water, and ε represented residual error in brood year i.

The most appropriate model was selected based on AICc, and model residuals were plotted and examined for normality (Shapiro-Wilk test), autocorrelation (acf), and influential outliers (Cook's distance).

Results

Between-sex differences in freshwater growth

We found no significant difference in the size of the freshwater growth zone between sexes across brood years. Neither ANOVA for age-1.3 FW1 nor age-2.3 FW1 was significant (F = 1.07, df = 26, P = 0.37; and F = 1.37, df = 27, P = 0.10, respectively). The ANOVA for age-2.3 FW2 indicated that the full model was significant (F = 1.79, df = 27, P < 0.001); however, a model comparison test between the full model and the model with the interaction term removed indicated that the interaction term was not significant (F = 1.22, df = 26, P = 0.20), suggesting that the FW2 growth zone size was not different between sexes among brood years. Considering the results of the ANOVAs for each age class and growth zone across brood years and that the difference in size of each freshwater growth zone was small (Table 2.2), growth zone measurements for males and females were combined for all remaining analyses.

Objective 1: Freshwater growth trends over time

Freshwater growth varied from year to year for both FW1 and FW2. When compared to the pre-stocking average (BY 1982-1987; 0.27 mm), FW1 was larger after fry stocking (BY 1988-2006; 0.31 mm; Fig. 2.3). Conversely, FW2 was smaller after fry stocking compared to the pre-stocking average (0.32 mm and 0.36 mm, respectively; Fig. 2.4).

Objective 2: Density-dependent and climate effects on freshwater growth

We found no evidence that the number of stocked fry influenced the average amount of growth obtained in the first year of freshwater rearing, and limited evidence that it affected growth during the second year of growth. Variables pertaining to density dependence (number of stocked fry and adult escapement) did not appear in the top models for average FW1 (Table 2.3). The number of stocked fry during the first year did appear in the top models for FW2 (with negative coefficients, as predicted), but those models performed little better than the null model for FW2 (Table 2.3). The top models for both FW1 and FW2 included variables related to climate in the winter preceding the growth (WPDO for FW1 and WNPGO for FW2), but these variables added modest explanatory value over the null models (adjusted $R^2 \leq 0.15$; Table 2.3).

The models with the lowest AICc values for both freshwater growth zones adhered to normality assumptions (Shapiro-Wilk: $P = 0.30$ for FW1 and $P = 0.77$ for FW2). Model residuals for the best model selected for FW1 and FW2 are provided in Appendices B-1 and B-2, respectively. Plots used in visual assessment of the assumptions of all models with ΔAICc < 2 for FW1 and FW2 are given in Appendices B-3 and B-4, respectively.

Objective 3: Density-dependent effects on age at smoltification

The proportion of age-2 Sockeye Salmon smolts decreased after fry stocking (Fig. 2.5). We found a weakly negative relationship between adult escapement and proportion of age-2 smolts ($P = 0.02$). The model adhered to normality assumptions (Shapiro-Wilk: $P = 0.36$). Model residuals and plots used in visual assessment of the assumptions are shown in Appendices B-5 and B-6, respectively. However, ANOVA comparison of the model containing adult escapement with the null model indicated the escapement model did not add explanatory power over the null model (Chi square: $P = 0.01$).

Discussion

The goal of our study was to determine whether stocking of Sockeye Salmon fry resulted in decreased freshwater growth due to density-dependent processes. Using an existing scale archive comprised of adult Sockeye Salmon scales collected over three decades, we strove to account for potential climate influences as well as increased fish density during the period of fry stocking. This longer frame of reference was important for determining the range of natural variation in freshwater growth prior to stocking as several major climate events occurred around the same time as major fry stocking efforts (e.g., El Niño), making it difficult to isolate the effects of hatchery activities on the growth of juvenile Sockeye Salmon in Chilkat Lake.

This study placed a previous finding (Eggers et al. 2008) of reduced Sockeye Salmon smolt size following increased fry density in Chilkat Lake into a longer time frame, allowing for examination of normal freshwater growth conditions prior to enhancement activities as well as additional years following discontinuation of fry stocking. We hypothesized that the results of this study would yield similar results, specifically that 1) freshwater growth would be negatively correlated with variables expressing density dependence (i.e., number of stocked fry and adult escapement), and 2) age at smoltification would increase (i.e. greater proportion of age-2 smolts) after fry stocking. However, we found limited or contrary evidence for these hypotheses.

We found little support for hypotheses 1 for the first year of freshwater growth. Model results suggested the opposite of our hypothesis in that average growth during the first freshwater year increased following fry stocking and was not correlated with any of the density-dependent variables, though results suggested a weak negative relationship with climate (WPDO). Average growth during the second year of fresh water suggested a declining trend following years of enhancement activities, which supported hypothesis 1; however, model results showed a weak negative relationship with the number of stocked fry and the climate variable WNPGO. Similarly, we found little support for hypothesis 2, detecting a weak negative relationship between adult escapement and age at smoltification. Specifically, the proportion of age-2 smolts decreased in the years following fry stocking, which was the opposite of expectation.

The timing of the Chilkat Lake fry stocking program coincided with several years of record high adult Sockeye Salmon escapement as well as several El Niño events, including a very strong El Niño in 1997/1998, prompting the inclusion of density-independent environmental variables into the models. Climate events, such as El Niño, can affect lake environments by changing the timing of spring ice breakup and affecting zooplankton prey densities (Schindler et al. 2005; Tillotson and Quinn 2016). These events may have had unexpected effects on freshwater rearing conditions, including potential density-dependent effects resulting from climate influences on wild spawner abundance (Mantua et al. 1997), tempering the conclusion that decreases in smolt size and increase in age at smoltification were a direct result of fry stocking and contributing to the variable results of this study.

A key limitation of our analyses is the use of an archived scale collection that represents only those individuals who survived to return to Chilkat Lake to spawn. An unavoidable downside is the loss of information from the component of the population that did not survive, which could be important when determining if stocking adversely affected juvenile growth and overall survival. The results of in-season monitoring of smolts as reported by Eggers et al. (2008) were derived from biological data (length, weight, age) collected directly from smolts captured as they left Chilkat Lake, while this study relied on measurements collected retrospectively from scales collected from surviving adults only. Unfortunately, scales from these smolts were not available, so we could not estimate a scale radius-smolt size relationship for back-calculating smolt size from the archived scales to directly compare size of the freshwater growth zones of the smolt scales versus scales from surviving adults. Using archived collections can present additional challenges that sometimes are not apparent prior to committing to the project such as gaps in the data (e.g., scale collections missing for entire years or lack of scales available to measure due to resorption or poor sampling techniques), resulting in a discontinuous time series. Unfortunately, in this analysis of a rather short fry-stocking program, the gaps coincided with years of increased fry density, limiting our ability to evaluate effects on the juvenile freshwater growth stage. A single definitive factor or combination of factors affecting juvenile Sockeye Salmon scale growth proved to be difficult to ascertain. There may have been multiple interacting mechanisms influencing scale growth that were not accounted for in the models, or even when included it was difficult to gauge the level of influence, if any, of the individual variables due to events occurring simultaneously (e.g., high adult escapement and strong weather patterns). Additionally, estimating Sockeye Salmon fry density proved challenging due to a lack of direct measurements of wild fry. As a result, density-dependence in the model was represented by number of stocked fry and adult escapement, which may not have been the most appropriate variables to use.

Ultimately, the combination of factors made it difficult to answer specific research questions or confidently explain why the results did not support our hypotheses. The usefulness of long-term scale archive collections should still be considered for studies similar to this where the ability to examine a period of a fish's life history is an important tool in managing a population. The ability to reconstruct an entire time-series allows the researcher to develop an understanding of normal growth conditions making it easier to identify changes in growth and productivity and examine effects of a disruption to the system, either human- or environmental-induced.

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Figures

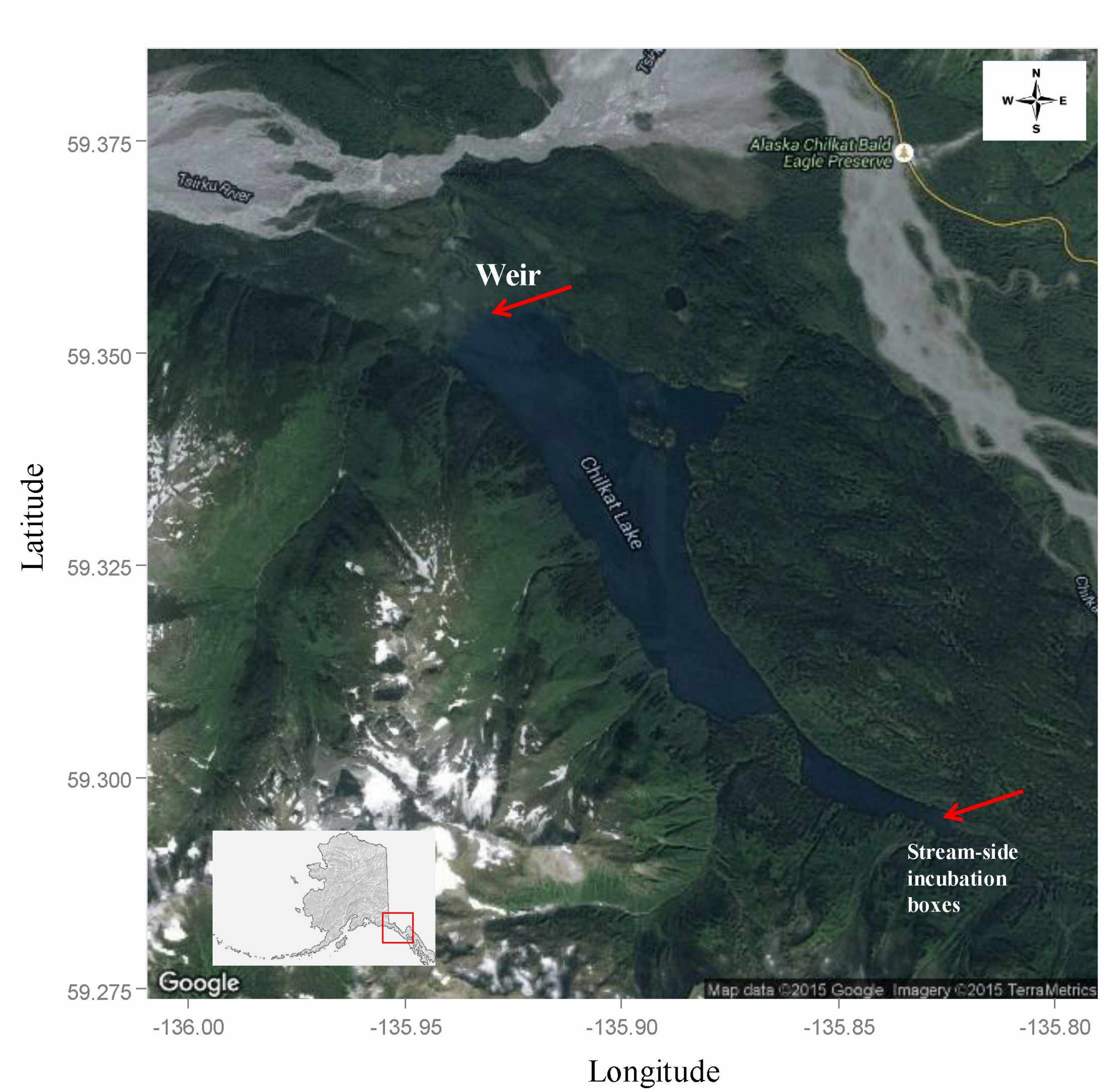

Figure 2.1. Map of Chilkat Lake including location of adult salmon weir and stream-side Sockeye Salmon incubation boxes.

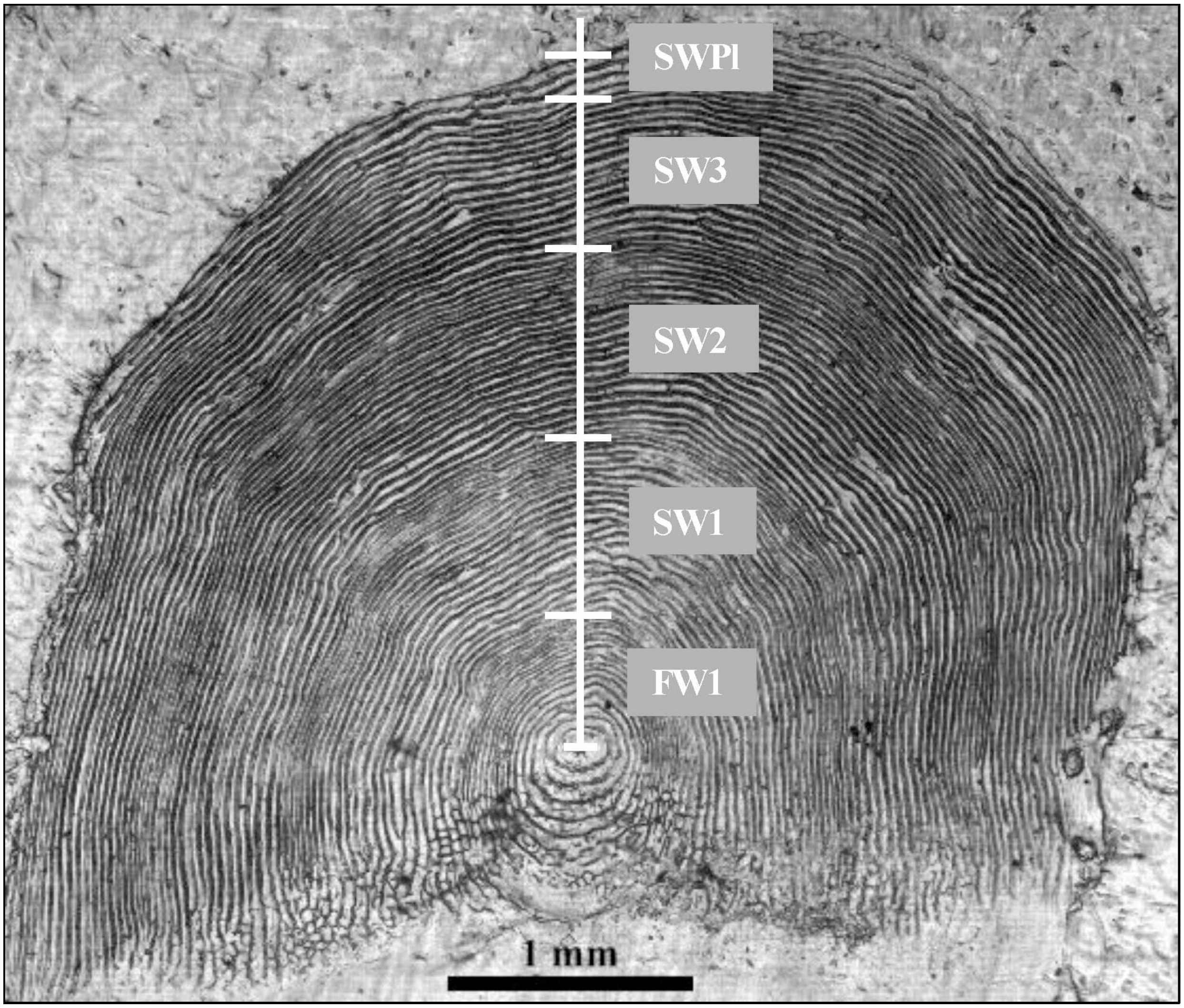

Figure 2.2. Age-1.3 (European) Sockeye Salmon scale from Chilkat Lake annotated with freshwater (FW) and saltwater (SW) growth zones.

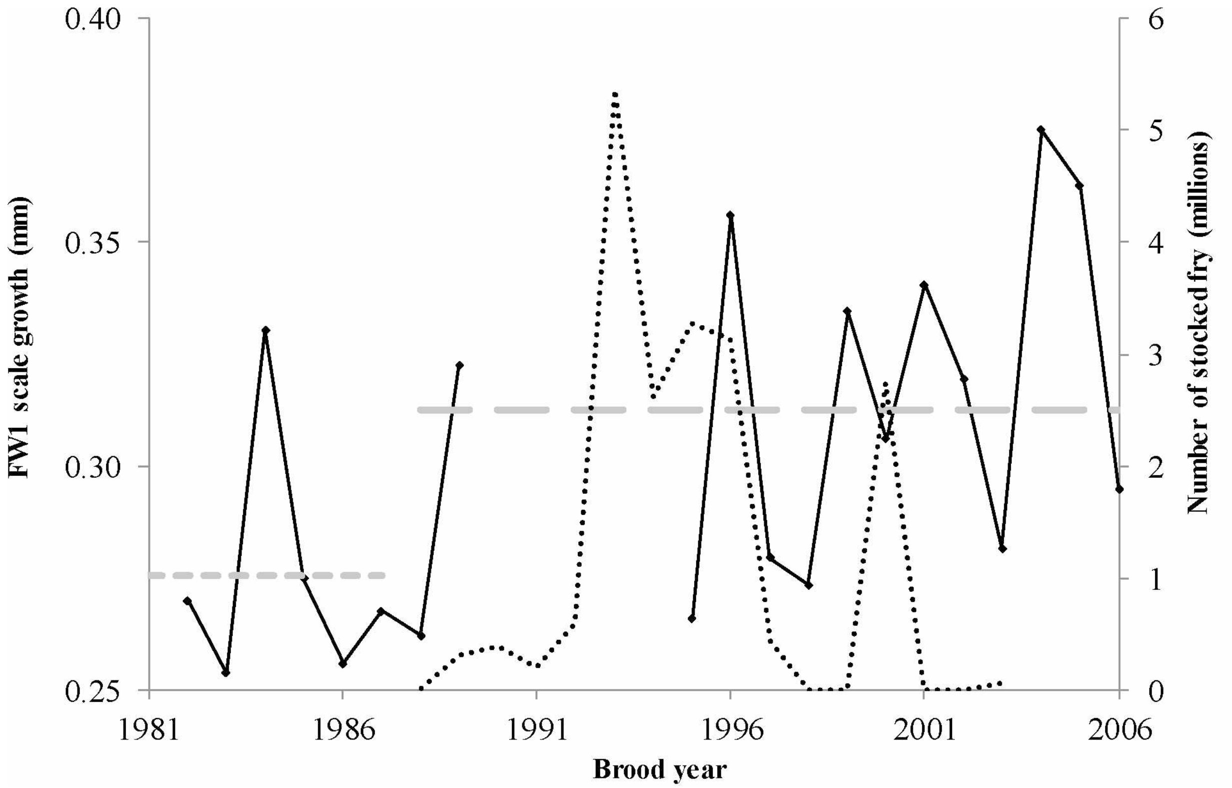

Figure 2.3. Average growth in the first year of fresh water (FW1) of juvenile Chilkat Lake Sockeye Salmon for brood years 1982-2006 (black line; data missing for brood years 1973-1981 and 1990-1994) in relation to numbers of stocked Sockeye Salmon fry (dotted line). Dashed grey horizontal lines represent average pre- (small dash) and post- (large dash) stocking values. FW1 is defined as the first year of freshwater growth regardless of freshwater age and was calculated by weighting the average FW1 growth by the freshwater age composition of each brood year (represented as the proportion of age-1.3 and -2.3 adult Sockeye Salmon from each respective brood year, calculated from the Chilkat Lake harvest and escapement brood table maintained by Alaska Department of Fish and Game).

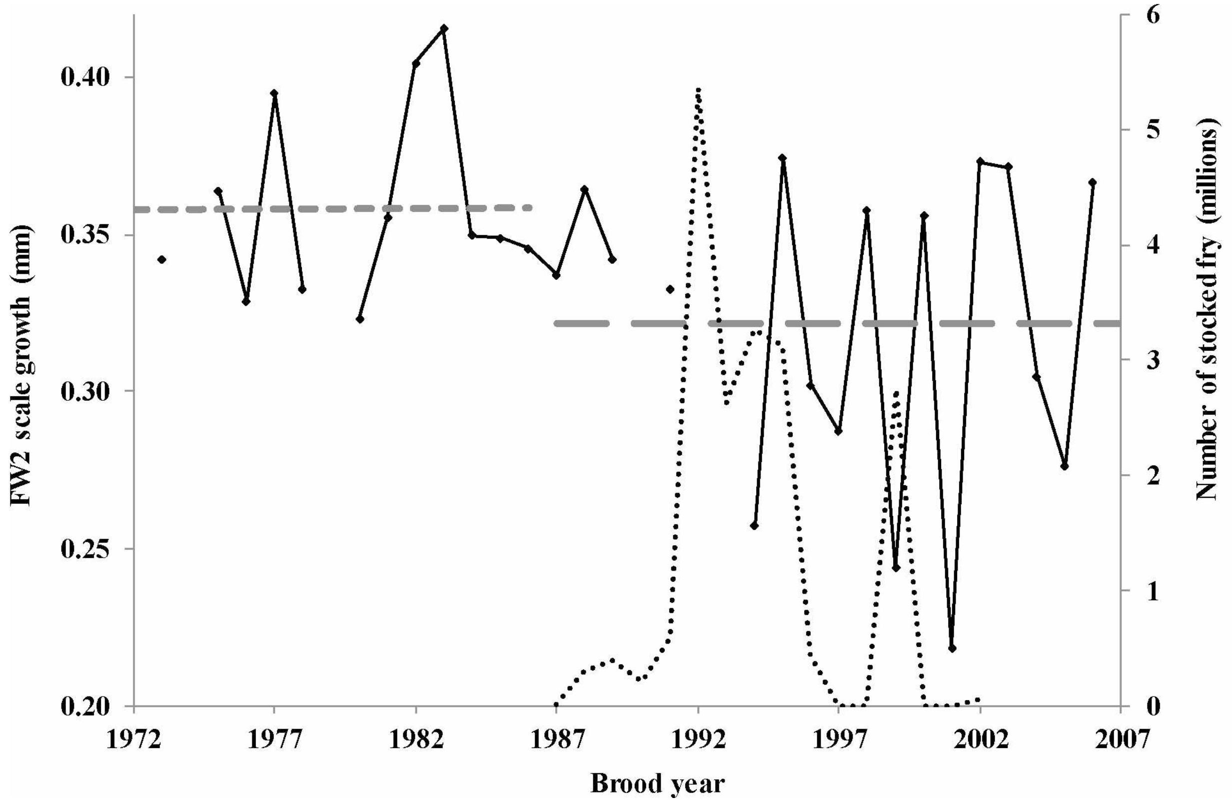

Figure 2.4. Average growth in the second year of fresh water (FW2) of age-2.3 juvenile Chilkat Lake Sockeye Salmon (FW2) for brood years 1973-2006 (black line; data missing for brood years 1974, 1979, 1990, 1992-1993) in relation to numbers of stocked Sockeye Salmon fry (dotted line). Dashed grey horizontal lines represent average pre- (small dash) and post- (large dash) stocking values.

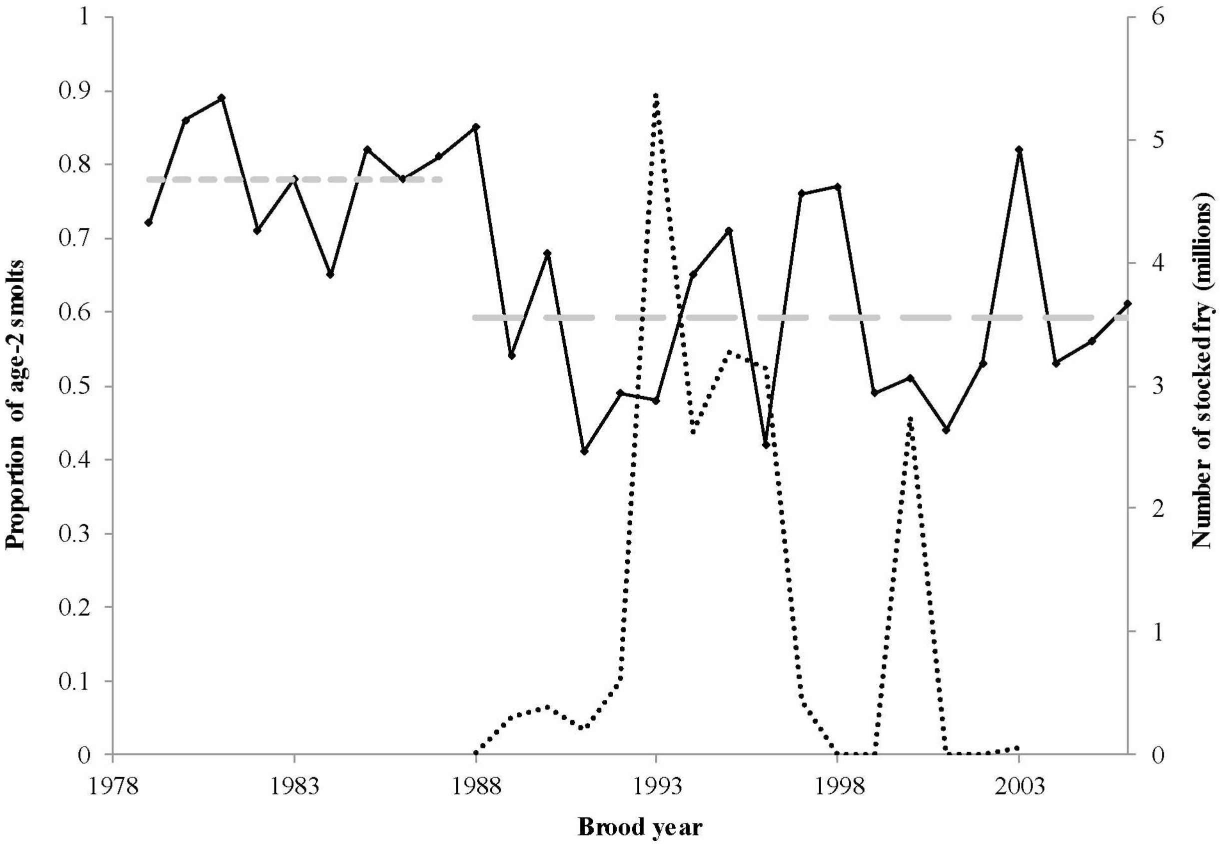

Figure 2.5. Proportion of age-2 Sockeye Salmon smolts that emigrated from Chilkat Lake for brood years 1979-2006 in relation to numbers of stocked Sockeye Salmon fry (dotted line), estimated from scales collected from adult Sockeye Salmon that returned to Chilkat Lake to spawn. Dashed grey horizontal lines represent average pre- (small dash) and post- (large dash) stocking values.

Tables

Table 2.1. Number of enhanced Sockeye Salmon fry released in Chilkat Lake from 1989-2004. Fry were released in spring, corresponding to the calendar year following the brood year.

Brood year	Stream-side incubation boxes[1]	Snettisham Hatchery[2]	Total	Type	Release wt. (g)
1988	15,094	0	15,094	Emergent	
1989	300,127	0	300,127	Emergent	
1990	388,000	0	388,000	Emergent	
1991	201,753	0	201,753	Emergent	
1992	594,000	0	594,000	Emergent	
1993	550,700	4,817,929	5,368,629	Emergent	0.12
1994	289,500	2,334,264	2,623,764	Emergent	0.30
1995	572,350	2,697,449	3,269,799	Emergent	0.14
1996	96,500	3,038,171	3,134,671	Emergent	0.16
1997	437,950	0	437,950	Emergent	
1998	0	0	0		
1999	0	0	0		
2000	0	2,743,374	2,743,374	Fed	0.17
2001	0	0	0		
2002	0	0	0		
2003	49,500	0	49,500	Emergent	

[1] Small-scale fry stocking.
[2] Large-scale fry stocking.

Table 2.2. Mean freshwater scale growth (mm) and standard deviation of the mean (SD) of juvenile male (M) and female (F) Sockeye Salmon from Chilkat Lake for all brood years combined.

Age	Sex	N	Mean	SD
1.3 FW1	M	637	0.40	0.06
	F	662	0.41	0.06
2.3 FW1	M	636	0.23	0.06
	F	672	0.23	0.06
2.3 FW2	M	636	0.34	0.07
	F	672	0.33	0.07

Table 2.3. Top candidate models (ΔAICc < 2 from best model) that explain freshwater growth in juvenile Chilkat Lake Sockeye Salmon for the first year in fresh water (FW1; brood years 1982-2006) and the second year in fresh water for age-2.3 (FW2; brood years 1973-2006). Best model in bold determined by AICc (second-order Akaike information criterion). ΔAICc = individual model AICc minus the lowest AICc from all possible models, df = degrees of freedom, and *Adj* R^2 = coefficient of determination adjusted for number of parameters. A total of 256 models were evaluated. Full model included: total number of stocked fry in current and previous years ($Stocked_j$ and $Stocked_{j-1}$, respectively), adult escapement in current and previous years (Esc_j and Esc_{j-1}, respectively), spring/summer Pacific Decadal Oscillation (SSPDO), winter Pacific Decadal Oscillation (WPDO), winter North Pacific Gyre Oscillation (WNPGO), and El Niño–Southern Oscillation (ENSO).

Response variable	Candidate models	AICc	ΔAICc	df	*Adj* R^2
FW1	**0.30 - 0.01WPDO**	**-69.8**	**0.0**	**18**	**0.09**
	0.31 - 0.03ENSO	-69.6	0.2	18	0.09
	Null model	-69.5	0.3	NA	NA
	0.30 - 0.02WPDO - 0.01WNPGO	-67.9	1.9	17	0.10
FW2	**0.34 - 0.02$Stocked_j$ - 0.01WNPGO**	**-91.5**	**0.0**	**26**	**0.13**
	0.34 - 0.01$Stocked_j$	-91.4	0.1	27	0.07
	0.34 - 0.03ENSO - 0.02$Stocked_j$	-90.8	0.7	26	0.10
	Null model	-90.6	0.9	NA	NA
	0.34 - 0.02ENSO - 0.02$Stocked_j$ - 0.01WNPGO	-90.4	1.1	25	0.15
	0.34 - 0.04ENSO - 0.02$Stocked_j$ + 0.01SSPDO	-90.3	1.2	25	0.15
	0.34 - 0.01WNPGO	-90.2	1.3	27	0.03
	0.34 - 0.02$Stocked_j$ + 0.01SSPDO	-89.6	1.9	26	0.07

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Chapter 3: General Conclusions

This study examined juvenile Sockeye Salmon growth over three decades (1973-2006) by reconstructing a time series to evaluate changes in growth in response to both density-dependent (fry stocking and high adult escapement) and density-independent (climate variability) factors. Specifically, our goal was to determine whether stocking of fry resulted in decreased freshwater growth due to density-dependent processes by measuring archived fish scales collected from the dominant age classes (ages 1.3 and 2.3) of adult Sockeye Salmon returning to Chilkat Lake, Alaska. Using the size of the freshwater portion of the scale as a proxy for freshwater growth, we evaluated changes in growth over the entire time series prior to and after a short-term lake enhancement program. Fry stocking activities were discontinued after in-season monitoring indicated a density-dependent effect on juvenile Sockeye Salmon growth (Eggers et al. 2008; Duckett et al. 2010). We hypothesized that 1) freshwater growth would decrease, and 2) age at smoltification would increase following increased fry density; however, the results of these analyses varied.

We found little support for hypotheses 1 for the first year of freshwater growth. Model results suggested the opposite of the hypothesis in that average growth during the first freshwater year increased following fry stocking and was not correlated with any of the density-dependent variables, though results suggested a weak negative relationship with climate (WPDO). Average growth during the second year of fresh water for age-2 fish suggested a declining trend following years of enhancement activities, which supported hypothesis 1; however, model results showed a weak negative relationship with the number of stocked fry and the climate variable WNPGO. Similarly, we found little support for hypothesis 2, detecting a weak negative relationship between adult escapement and age at smoltification. We found that age at smoltification decreased rather than increased following years of high fry density.

The timing of the Chilkat Lake fry stocking program coincided with several years of record high adult Sockeye Salmon escapement as well as several El Niño events, including a very strong El Niño in 1997/1998, prompting the inclusion of density-independent environmental variables into the models. Climate variation can affect freshwater environments by changing the timing of spring ice breakup and changing the length of the growing season as well as affecting prey availability and density (Schindler et al. 2005; Griffiths et al. 2014; Tillotson and Quinn 2016). These events may have had unexpected effects on freshwater rearing conditions, including potential density-dependent effects resulting from climate influences on wild spawner abundance (Mantua et al. 1997), tempering the conclusion that decreases in smolt size and increase in age at smoltification were a direct result of fry stocking (Eggers et al. 2008) and contributing to the variable results of this study.

A single definitive factor or combination of factors affecting juvenile Sockeye Salmon scale growth proved difficult to ascertain; however, it is important to acknowledge several factors that could have affected the results. Using historical scale collections represented only individuals who survived to return to Chilkat Lake, resulting in the loss of information from the component of the population that did not survive, which could be important when determining if stocking adversely affected juvenile growth and overall survival. The results of in-season monitoring of smolts as reported by Eggers et al. (2008) were derived from biological data (length, weight, age) collected directly from smolts captured as they left Chilkat Lake, while this study relied on measurements collected retrospectively from scales collected from surviving adults only. Unfortunately, scales from these smolts were not available, so we could not estimate a scale radius-smolt size relationship for back-calculating smolt size from the archived scales to directly compare freshwater growth zone size of the smolt scales versus scales from surviving adults.

Another factor that should be considered is gaps in the data (e.g., scale collections missing for entire years or lack of scales available to measure due to resorption or poor sampling techniques), resulting in a discontinuous time series. In this analysis, where the duration of the fry-stocking program was relatively short, the gaps coincided with years of increased fry density, making it difficult to evaluate effects on the juvenile freshwater growth stage. Additionally, the duration of enhancement activities was relatively short in comparison to the length of the time series which could make identifying the cause of any kind of response, positive or negative, difficult to measure.

Variable selection may have also affected the results of our study. Our choice of climate metrics, based largely on availability across the time series, may not have adequately captured environmental influences freshwater growth and smolt age. Over the time series, unanticipated events (e.g., high adult escapement and strong weather patterns) occurred simultaneously with the focal management intervention (hatchery supplementation), leading to confounding influences that simply could not be disentangled with statistical models. Additionally, estimating Sockeye Salmon fry density proved challenging due to a lack of direct measurements of wild fry, and as a result density dependence in the model was represented by number of stocked fry and adult escapement, which may have not been the most appropriate variables to use.

Ultimately, confounding biological and environmental processes, coupled with unfortunately timed data gaps, made it difficult to unequivocally test our hypotheses or to confidently explain why the hypotheses were not supported. Long-term scale archive collections should still be considered useful for studies such as this where the ability to examine a particular period of a fish's life history is an important tool in managing a population. Previous studies have shown the validity of using reconstructed salmon growth time series to answer research questions (e.g. Ruggerone et al. 2007; Martinson et al. 2008; Agler et al. 2013; Siegel et al. 2017). The ability to reconstruct an entire time series allows the researcher to characterize normal growth patterns, making it easier to identify changes in growth and productivity and correlate changes to a disruption in the system, either human- or environmental-induced.

Our study highlights the importance of having a monitoring plan in place well in advance of management interventions. It is necessary to understand the range of natural variation to be able to understand the effectiveness, or possible negative consequences, of management activities. Long-term monitoring requires consistency in data collection methods and management oversight. Changes made during the course of the project can affect future uses of the data. For example, this study was affected by gaps in the time series due partly because the scale collection method was modified for a few years and then returned to the original method. Often management actions are based on available funds resulting in unavoidable breaks in data collection; however, whenever possible keeping project methodology consistent is best. This study was not able to conclude with certainty that fry stocking negatively affected juvenile freshwater Sockeye Salmon growth, and as evidenced by the spawner recruit plot (Steve Heinl, pers. comm.; Appendix C-1) that shows that Chilkat Lake had yet to rebound several years after the end of the stocking program, there may be other factors affecting Sockeye Salmon production. Future examination of marine growth zones may present a more complete picture of factors affecting Chilkat Lake Sockeye Salmon growth and survival.

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Appendices

Appendix A

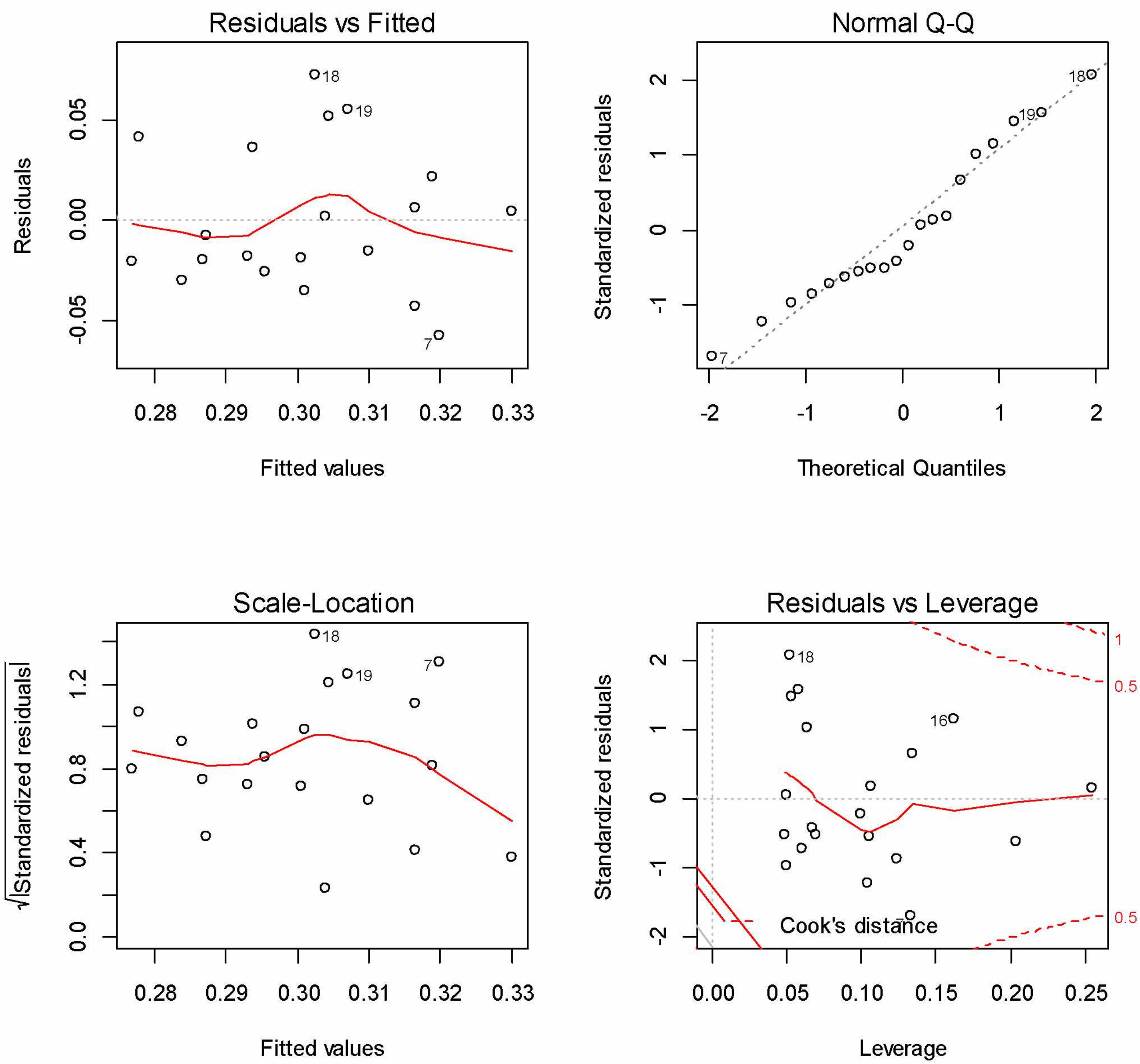
Appendix A-1. Sample size, by age class and sex, of adult Sockeye Salmon scales collected at Chilkat Lake used in a study of freshwater growth from brood years 1973-2006.

	Age 1.3				Age 2.3			
BY	Male	Female	Unknown	Total	Male	Female	Unknown	Total
1973			29	29			22	22
1974			50	50				0
1975			27	27	29	16		45
1976	25	25		50	25	24		49
1977	25	26		51	24	25		49
1978	25	25		50	25	24		49
1979	25	25		50				0
1980				0	14	33		47
1981				0	26	24		50
1982	25	25		50	25	25		50
1983	25	25		50	22	24		46
1984	25	25		50	21	25		46
1985	25	25		50	25	25		50
1986	25	25		50	25	24		49
1987	25	25		50	25	25		50
1988	25	25		50	25	25		50
1989	25	25		50	24	26		50
1990	25	25		50				0
1991				0	2	17		19
1992	8	7		15				0
1993	4	8		12				0
1994				0	25	25		50
1995	24	24		48	23	26		49
1996	25	25		50	23	28		51
1997	24	24		48	25	25		50
1998	23	26		49	25	24		49
1999	26	26		52	24	25		49
2000	22	26		48	24	23		47
2001	25	32		57	24	26		51
2002	20	28		48	16	20		36
2003	24	25		49	20	26		46
2004	25	24		49	25	29		54
2005	25	25		50	24	25		49
2006	23	27		50	23	25		48

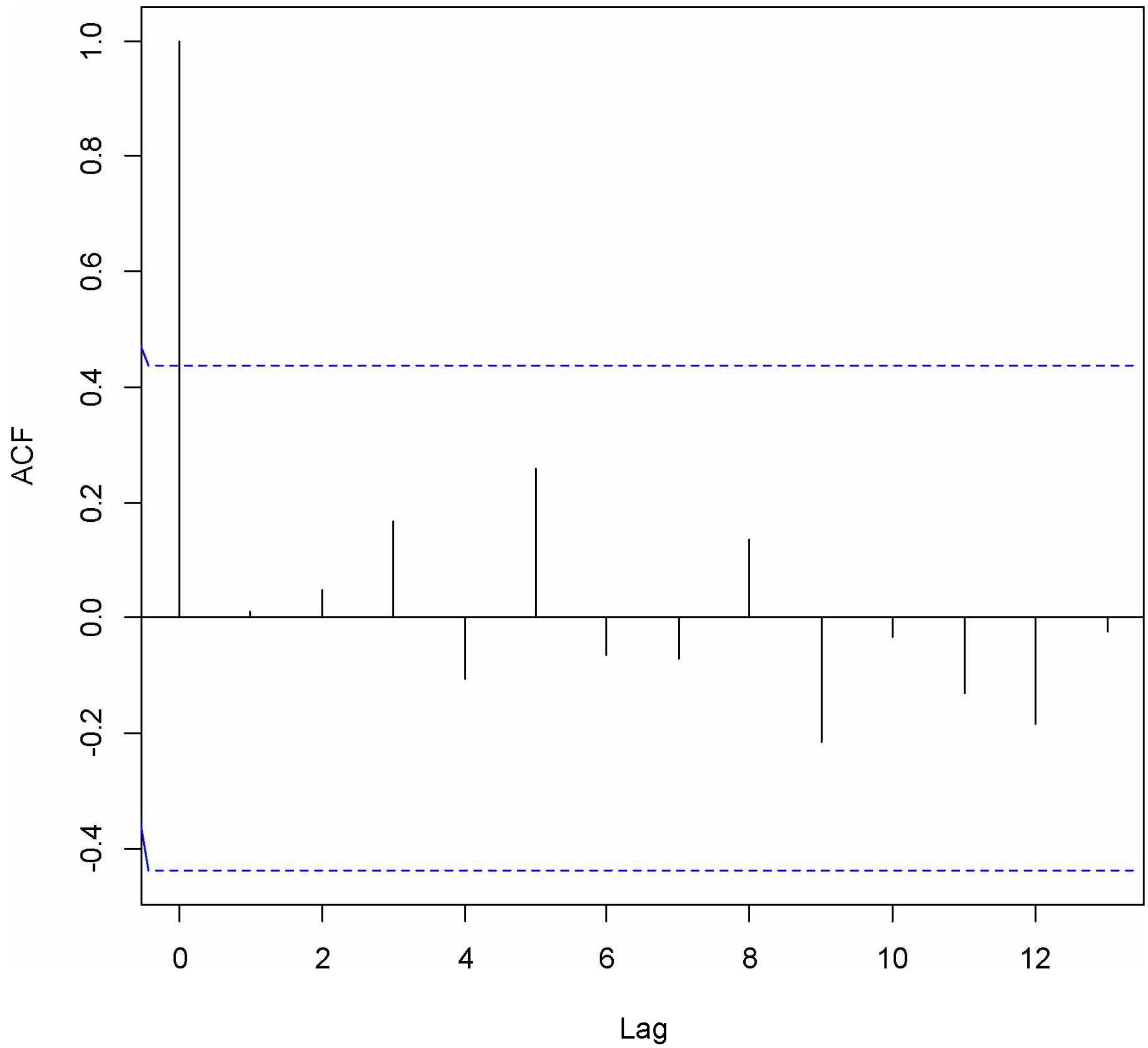
Appendix A-2. Correlation coefficient matrix for environmental variables used to evaluate changes in freshwater growth of Chilkat Lake juvenile Sockeye Salmon. Environmental variables include spring/summer and winter Pacific Decadal Oscillation (SSPDO and WPDO, respectively) and winter North Pacific Gyre Oscillation (WNPGO).

	SSPDO	WPDO	WNPGO
SSPDO	—		
WPDO	0.57	—	
WNPGO	-0.52	-0.07	—

Appendix B

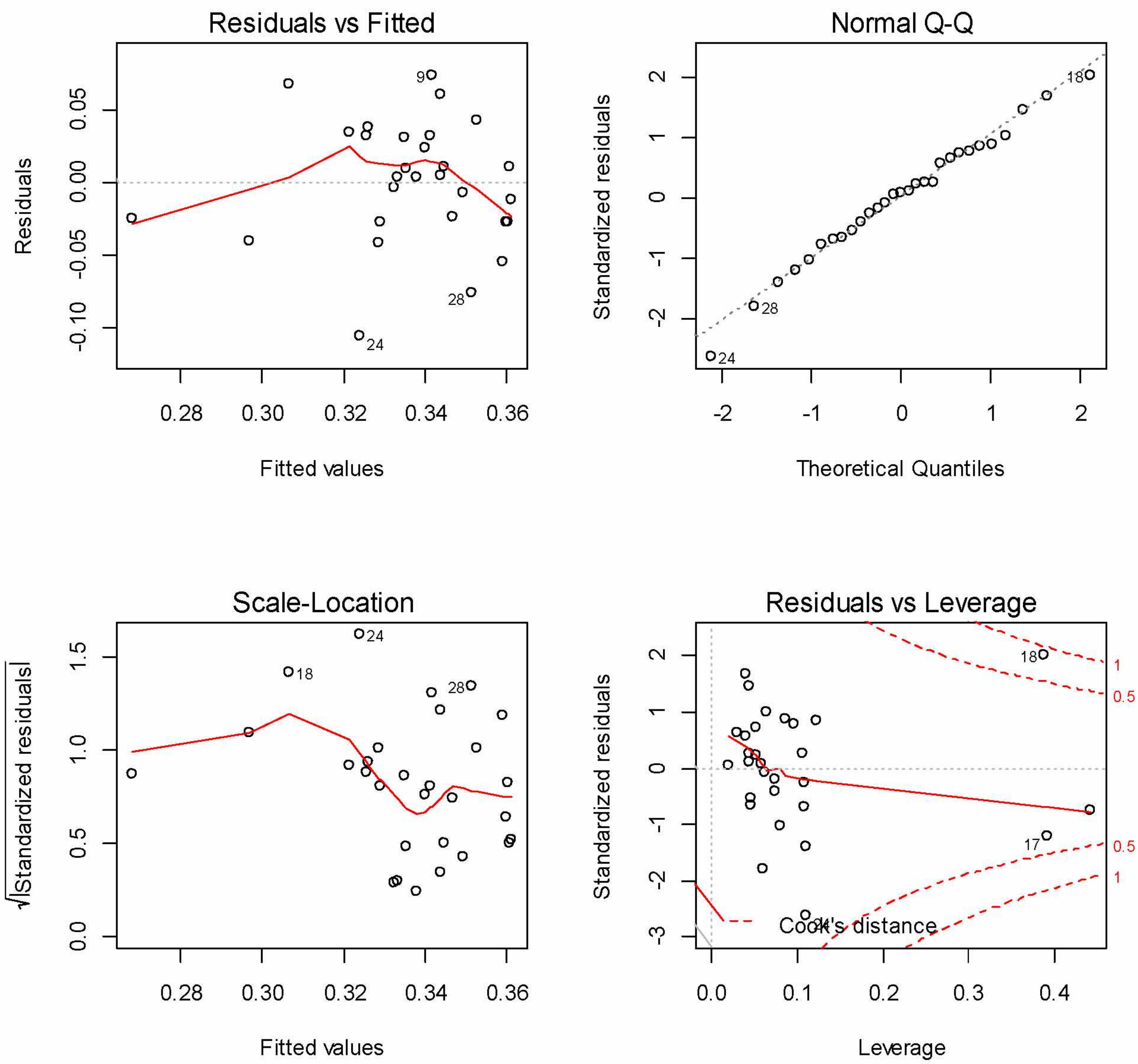

Residuals vs Fitted
Normal Q-Q
Scale-Location
Residuals vs Leverage
Residuals
Fitted values
Standardized residuals
Theoretical Quantiles
√|Standardized residuals|
Leverage
Cook's distance

(a)

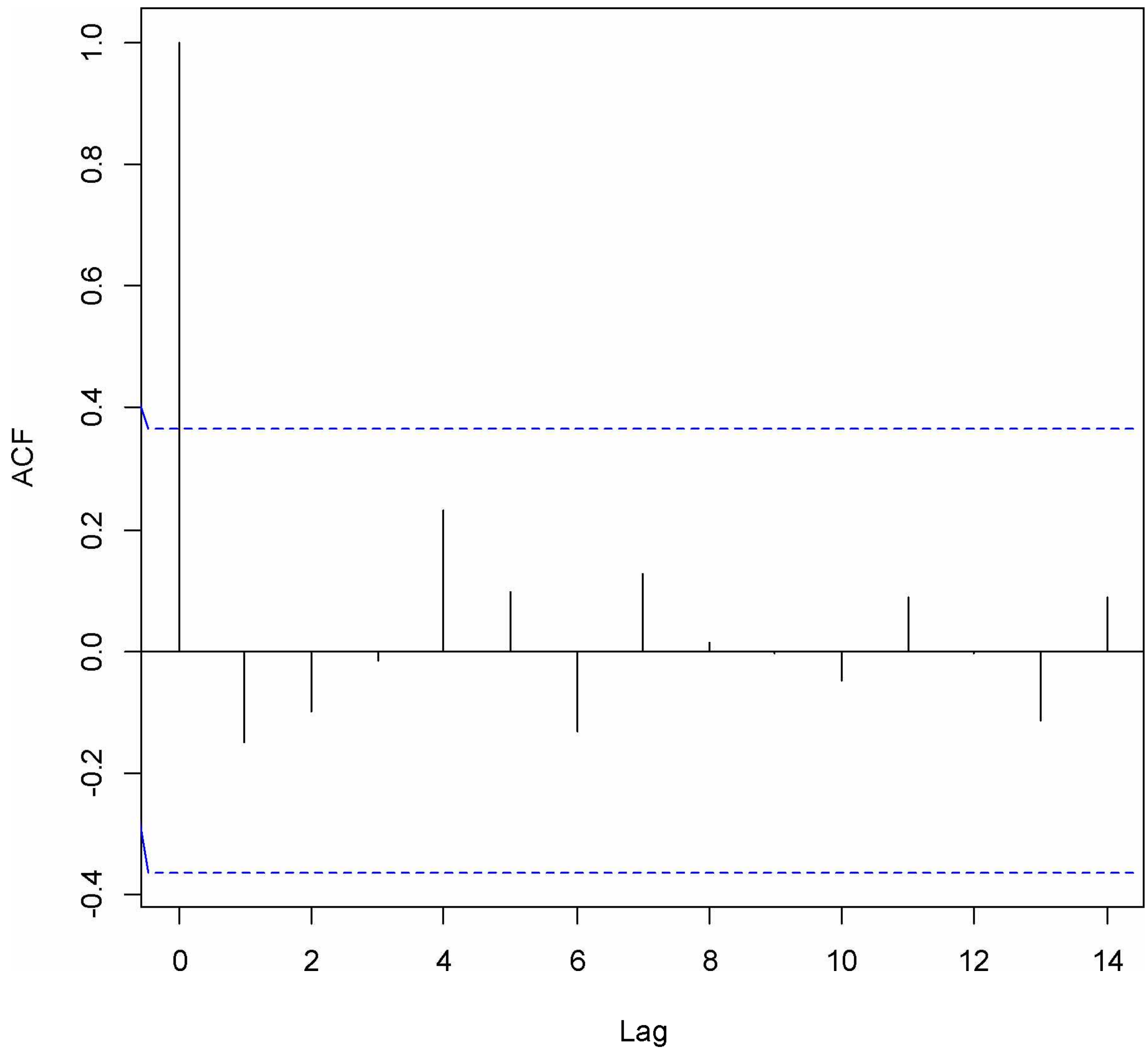


(b)

Appendix B-1. Model residuals **(a)** and autocorrelation plot **(b)** for the best model (chosen by AICc) to explain variation in the first year of freshwater (FW1) scale growth of juvenile Chilkat Lake Sockeye Salmon for brood years 1982-2006. FW1 is defined as the first year of freshwater growth, regardless of freshwater age, and was calculated by weighting the average FW1 growth by the freshwater age composition of each brood year (represented as the proportion of age-1.3 and -2.3 adult Sockeye Salmon from each respective brood year, calculated from the Chilkat Lake harvest and escapement brood table maintained by Alaska Department of Fish and Game).

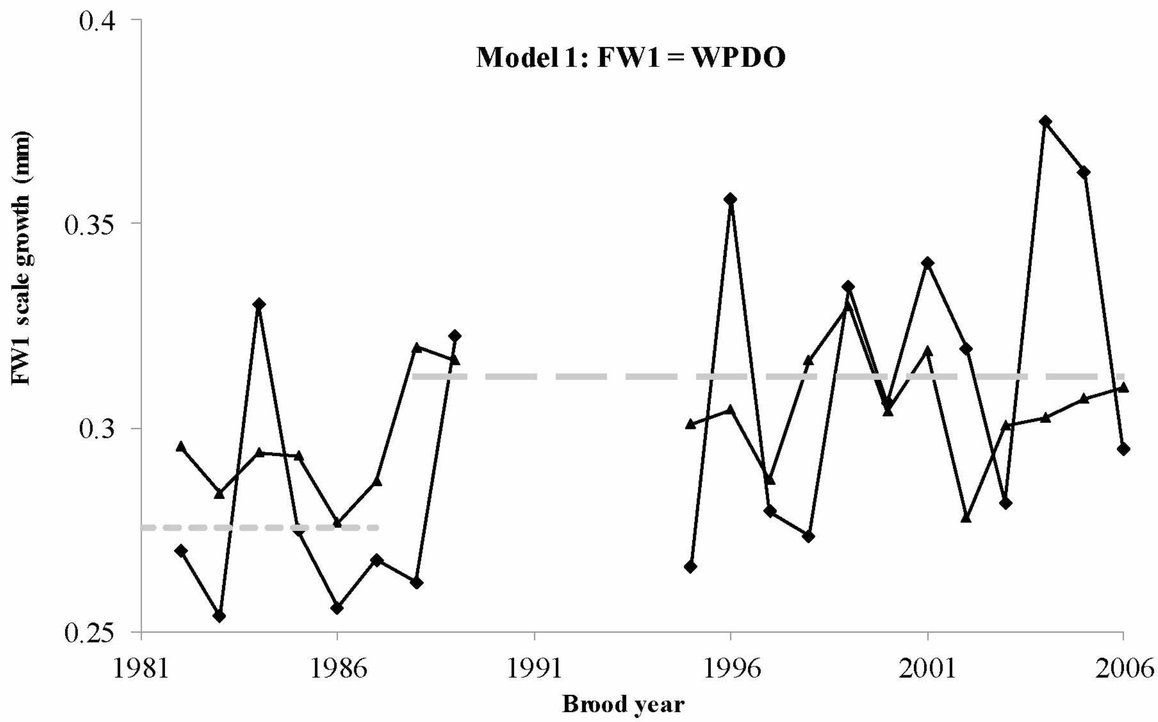

Residuals vs Fitted
Residuals
Fitted values
Normal Q-Q
Standardized residuals
Theoretical Quantiles
Scale-Location
√|Standardized residuals|
Fitted values
Residuals vs Leverage
Standardized residuals
Leverage
Cook's distance

(a)



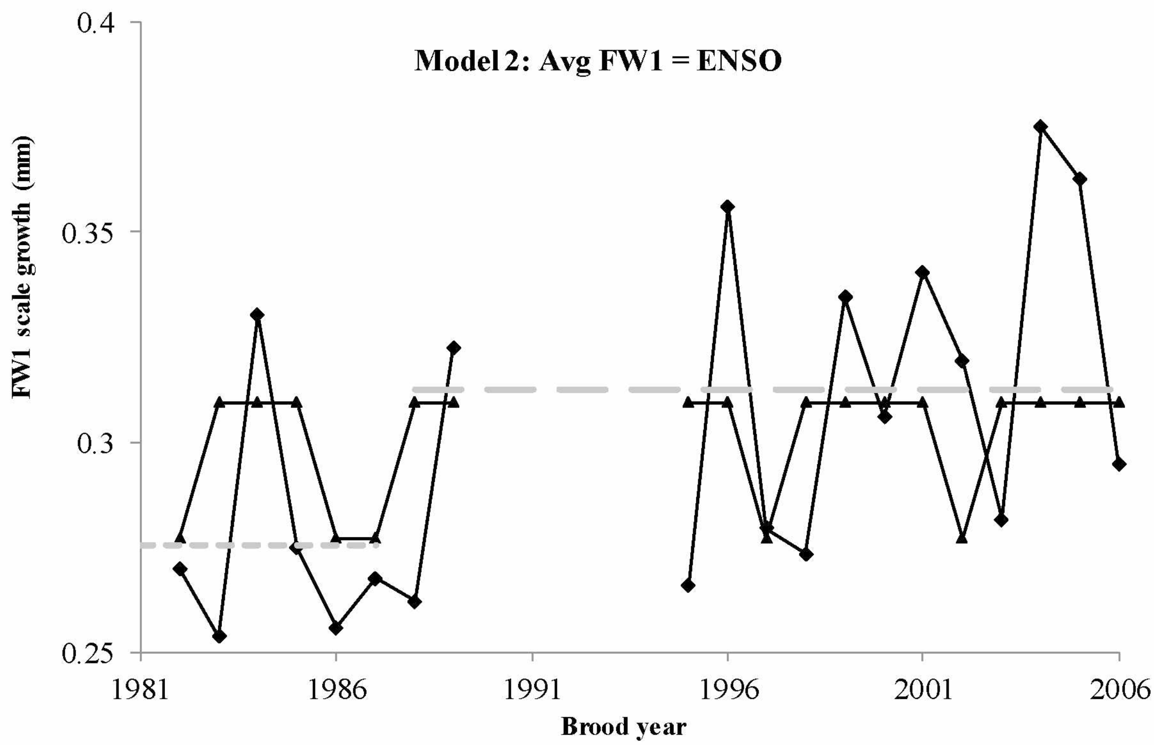
(b)

Appendix B-2. Model residuals **(a)** and autocorrelation plot **(b)** for the best model (chosen by AICc) to explain variation in the second year of freshwater (FW2) scale growth of juvenile Chilkat Lake Sockeye Salmon for brood years 1973-2006.



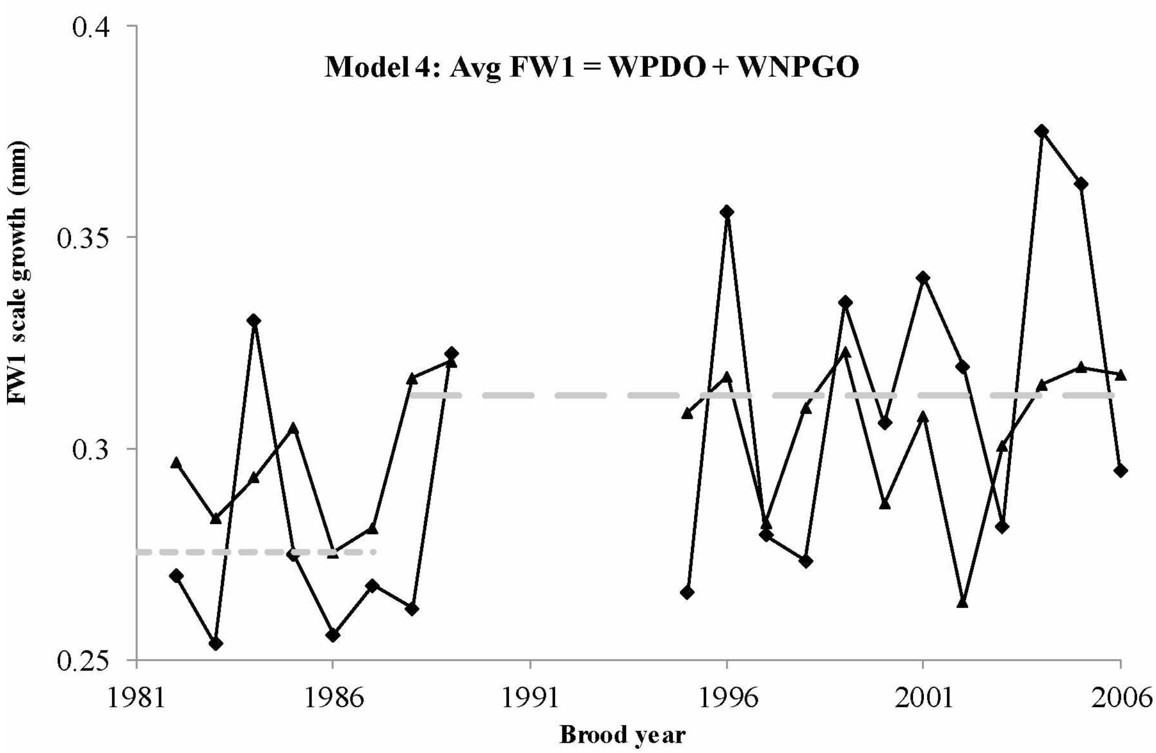
Model 1: FW1 = WPDO
FW1 scale growth (mm)
0.4
0.35
0.3
0.25
1981
1986
1991
1996
2001
2006
Brood year

(a)



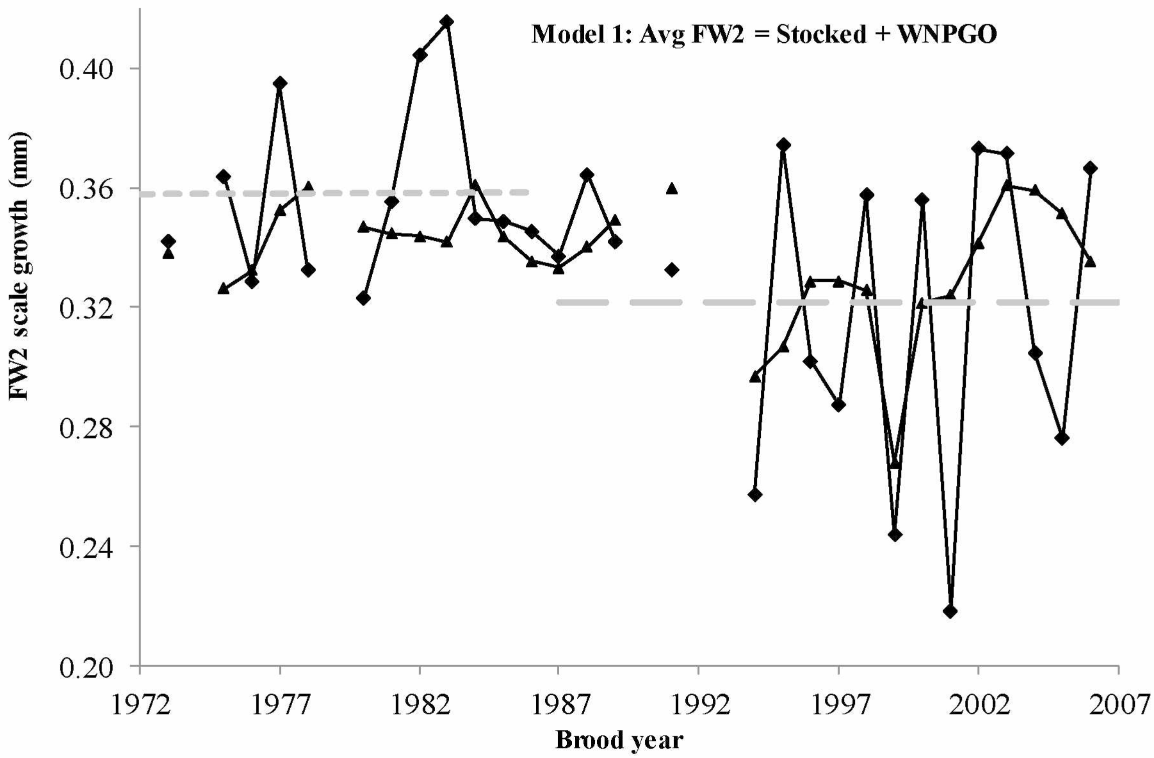
Model 2: Avg FW1 = ENSO
FW1 scale growth (mm)
0.4
0.35
0.3
0.25
1981
1986
1991
1996
2001
2006
Brood year

(b)

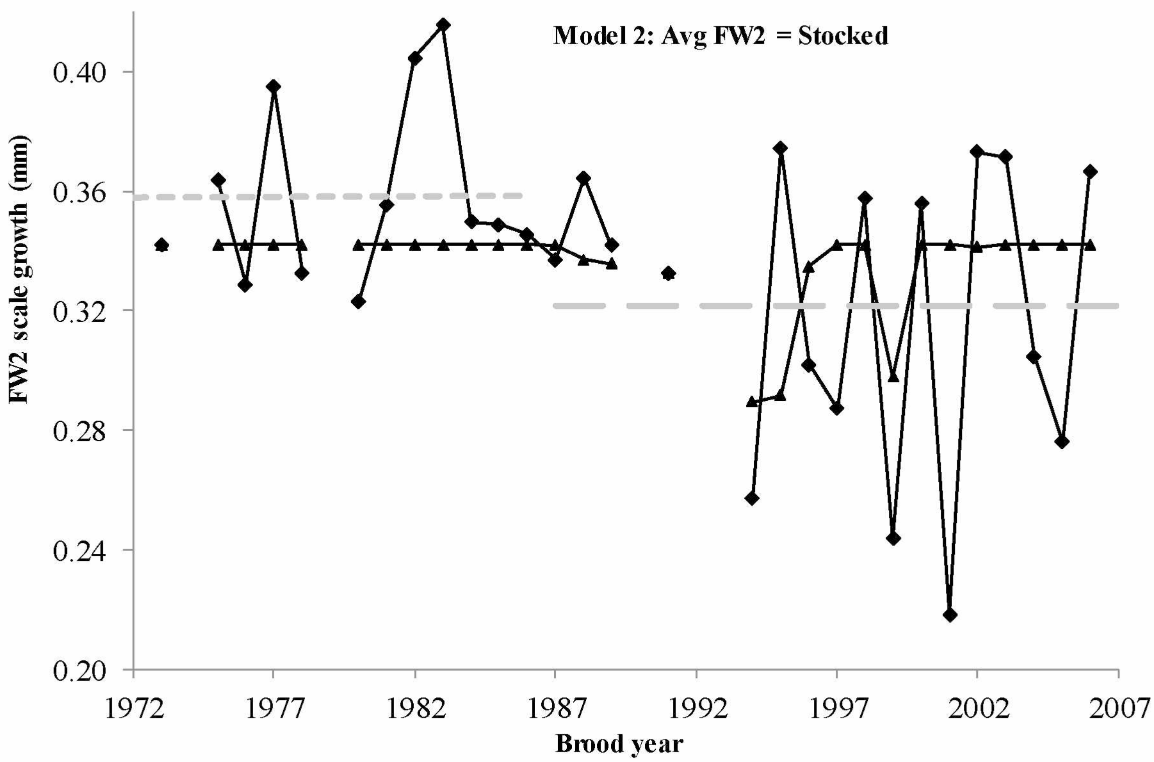


(c)

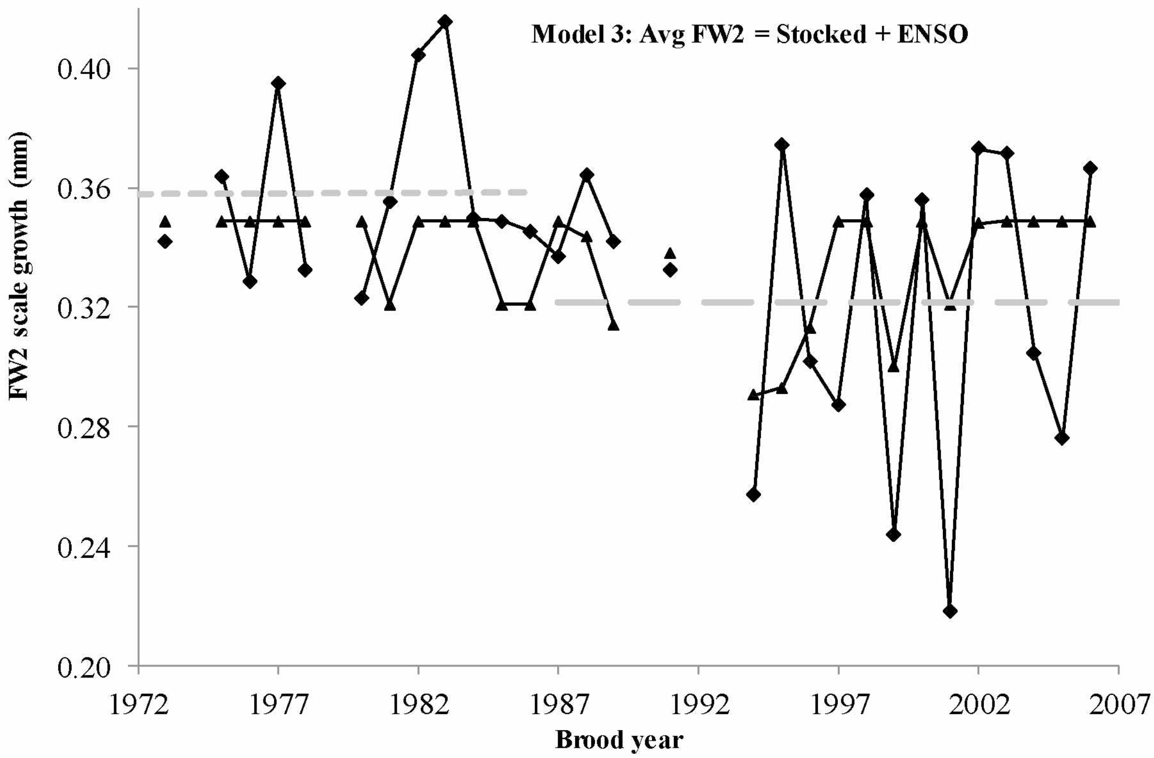
Appendix B-3. Observed (diamonds) versus predicted (triangles) growth in the first year of fresh water (FW1) for juvenile Chilkat Lake Sockeye Salmon for brood years 1982-2006 (missing data for brood years 1990-1994) for the top candidate models **(a)** Model 1, **(b)** Model 2, and **(c)** Model 4 (chosen by AICc) in relation to the pre- (small dashed line) and post- (large dashed line) stocking average values. Model 3 (Null model) is not included. FW1 is defined as the first year of freshwater growth regardless, of freshwater age, and was calculated by weighting the average FW1 growth by the freshwater age composition of each brood year (represented as the proportion of age-1.3 and -2.3 adult Sockeye Salmon from each respective brood year, calculated from the Chilkat Lake harvest and escapement brood table maintained by Alaska Department of Fish and Game.


Model 1: Avg FW2 = Stocked + WNPGO
FW2 scale growth (mm)
0.40
0.36
0.32
0.28
0.24
0.20
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

(a)

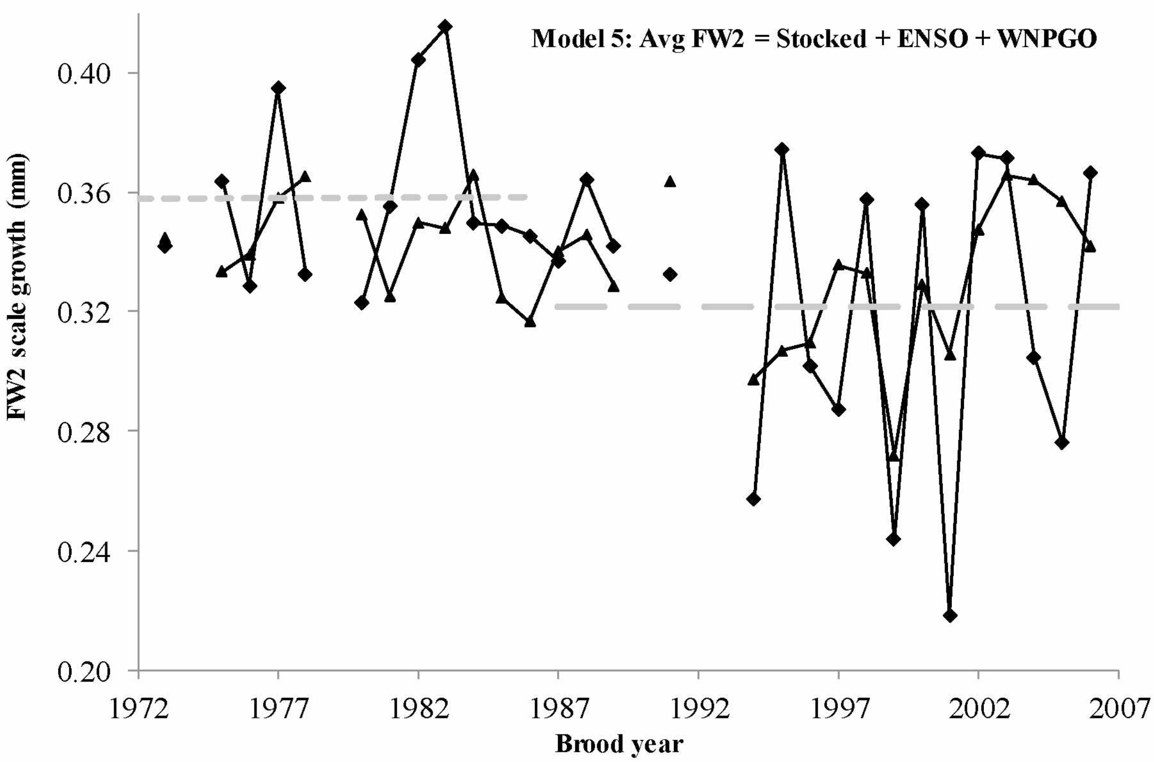

Model 2: Avg FW2 = Stocked
FW2 scale growth (mm)
0.40
0.36
0.32
0.28
0.24
0.20
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

(b)



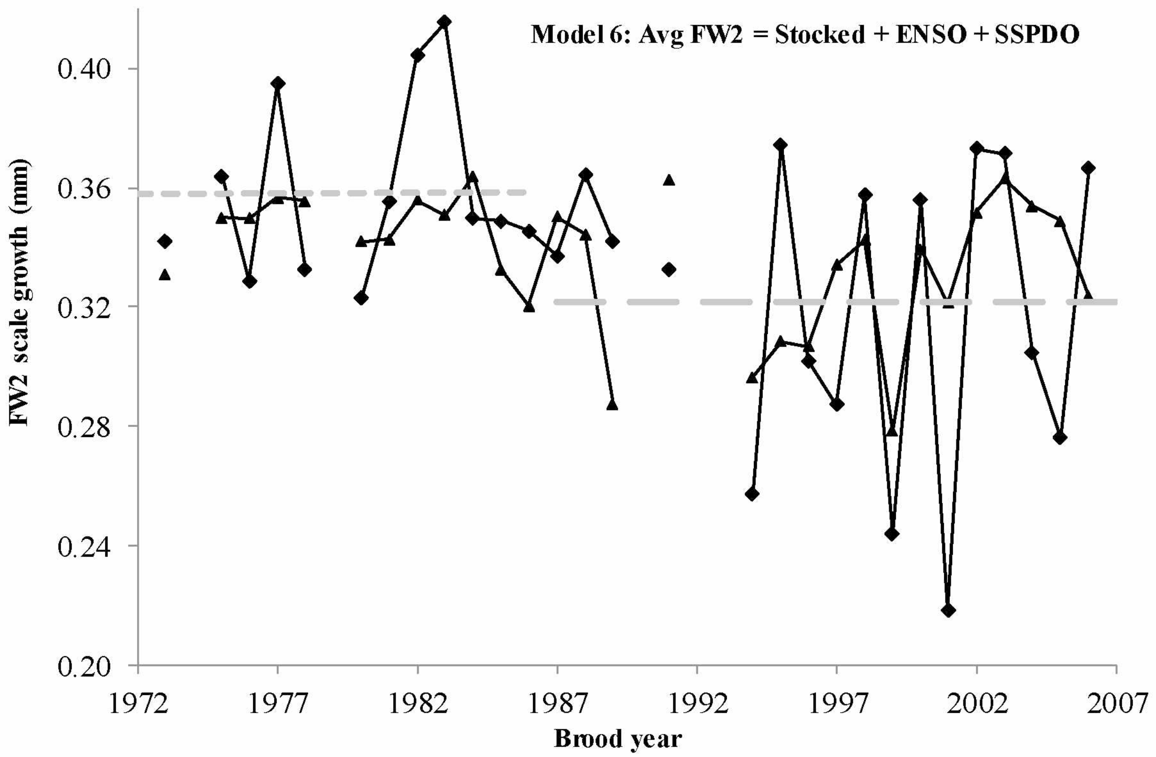
Model 3: Avg FW2 = Stocked + ENSO
FW2 scale growth (mm)
0.40
0.36
0.32
0.28
0.24
0.20
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

(c)

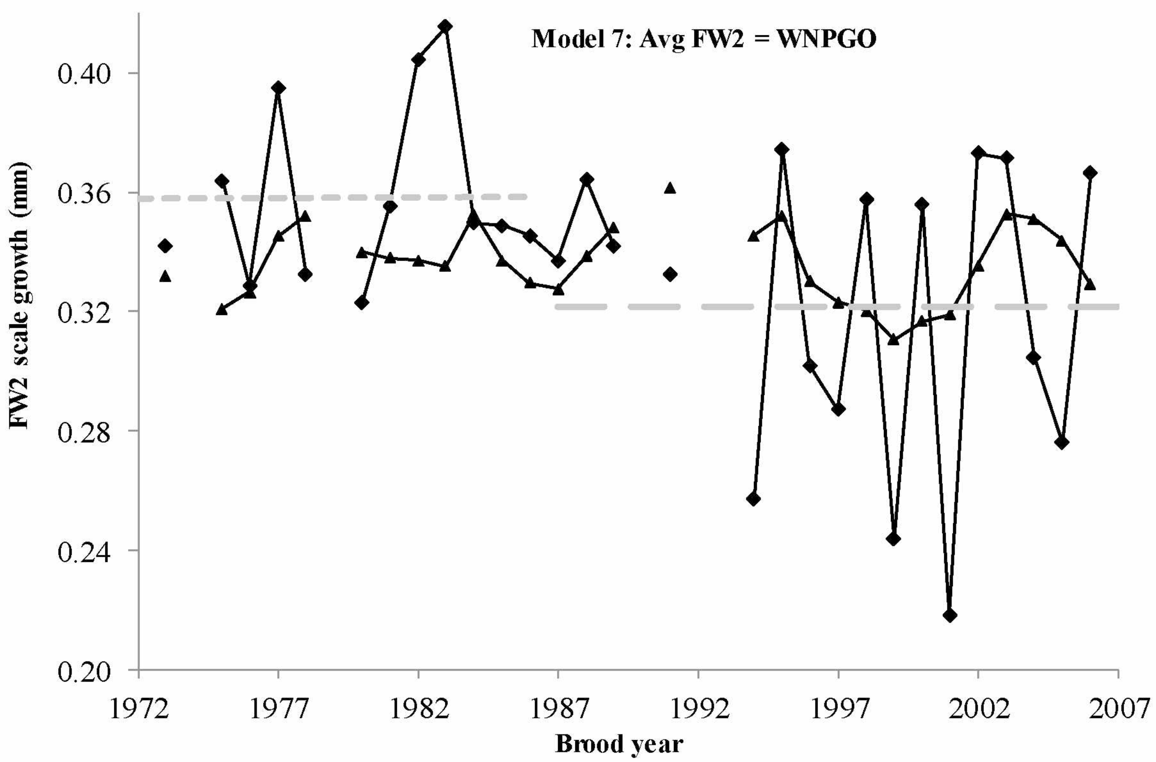


Model 5: Avg FW2 = Stocked + ENSO + WNPGO
FW2 scale growth (mm)
0.40
0.36
0.32
0.28
0.24
0.20
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

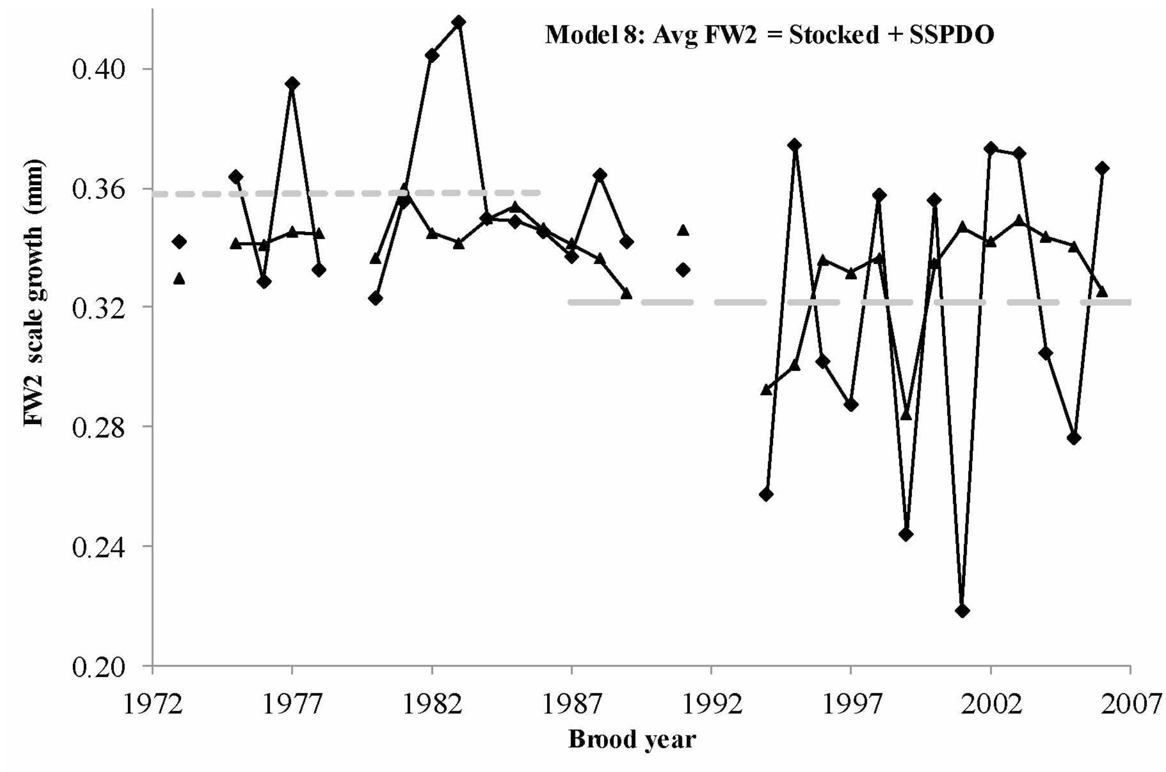
(d)


Model 6: Avg FW2 = Stocked + ENSO + SSPDO
FW2 scale growth (mm)
0.20
0.24
0.28
0.32
0.36
0.40
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

(e)

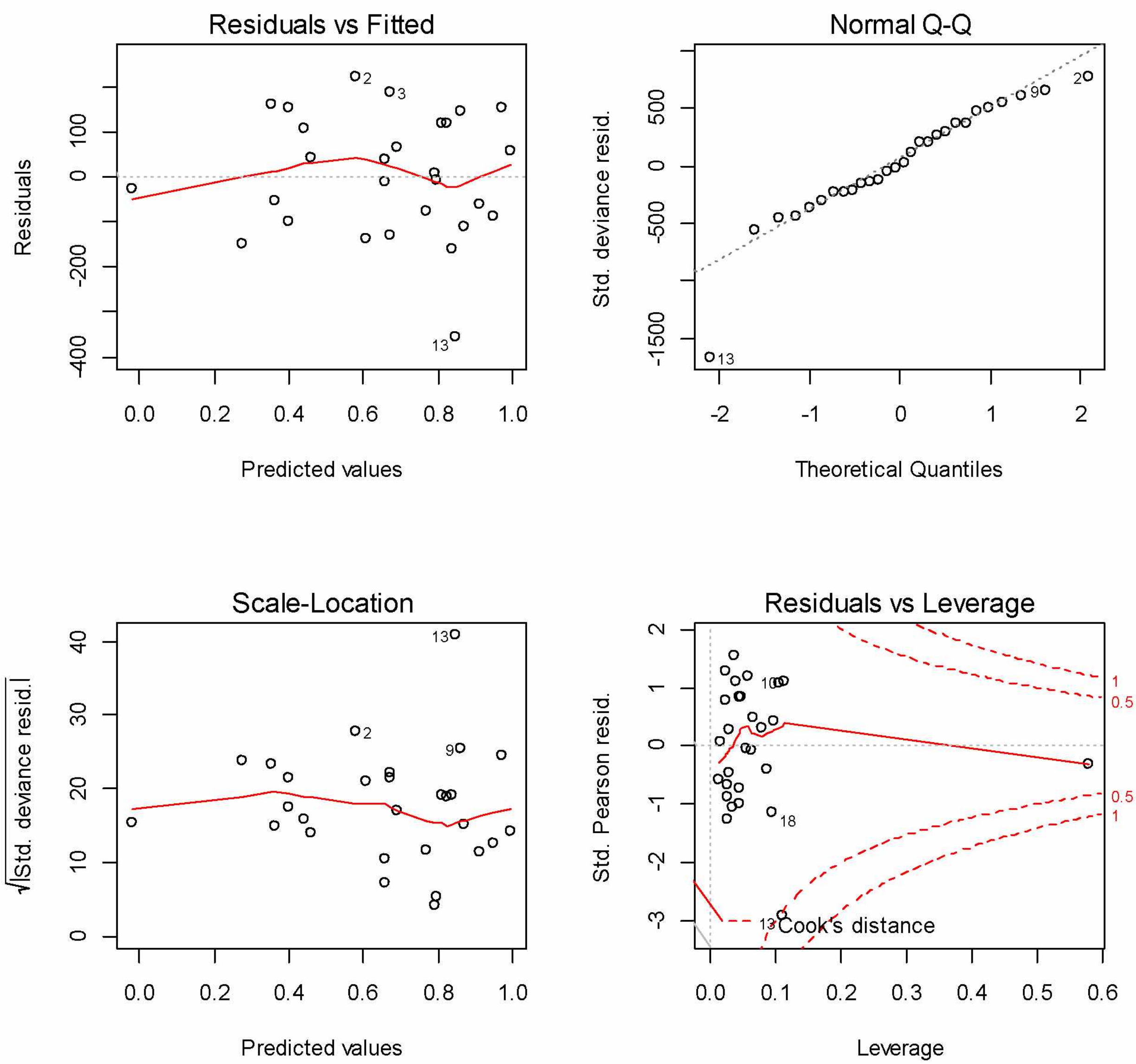

Model 7: Avg FW2 = WNPGO
FW2 scale growth (mm)
0.20
0.24
0.28
0.32
0.36
0.40
1972
1977
1982
1987
1992
1997
2002
2007
Brood year

(f)



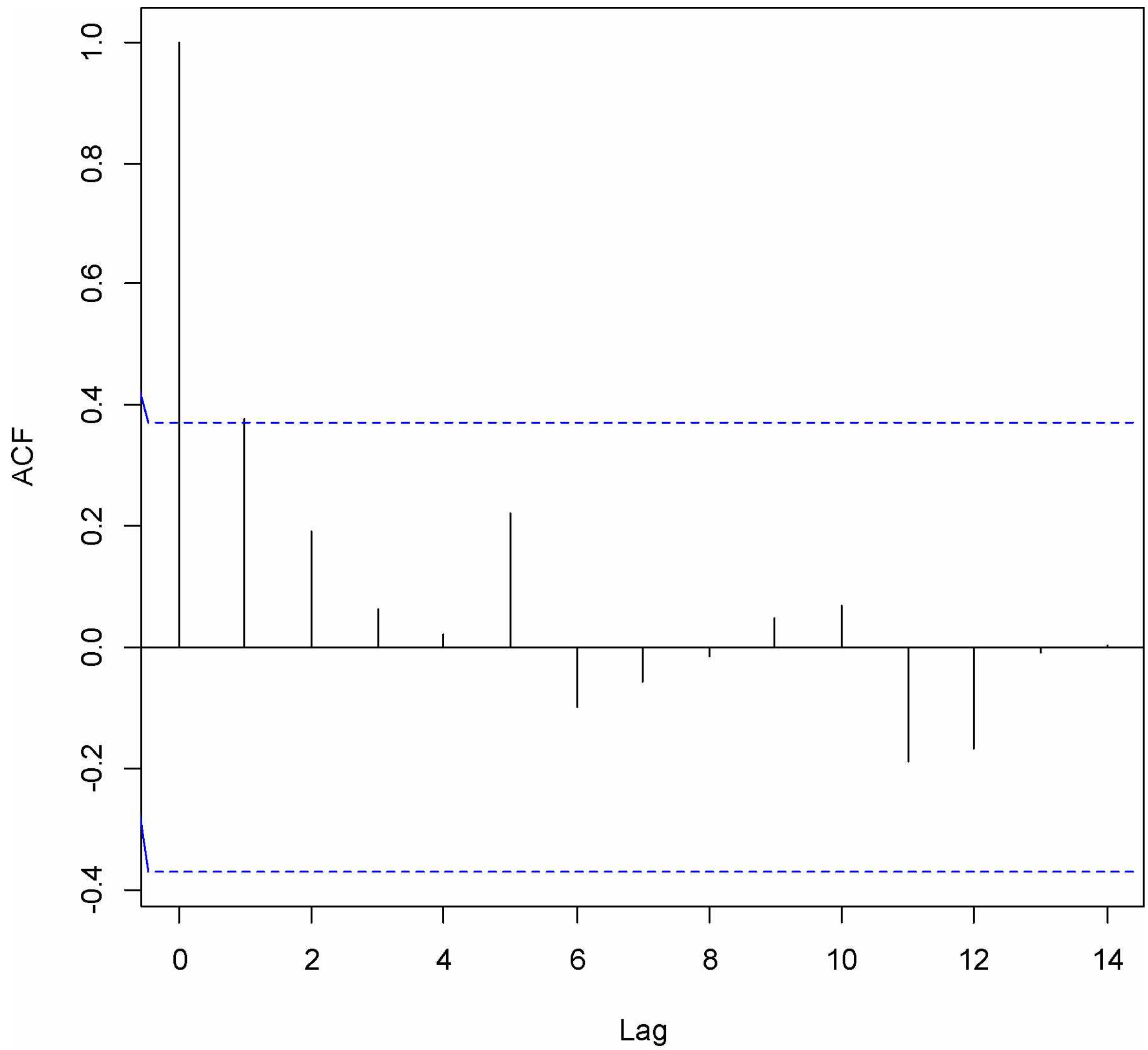
(g)

Appendix B-4. Observed (diamonds) versus predicted (triangles) growth in the second year of fresh water (FW2) for age-2.3 juvenile Chilkat Lake Sockeye Salmon for brood years 1973-2006 (missing data for brood years 1974, 1979, 1990, 1992, 1993) for the top candidate models **(a)** Model 1, **(b)** Model 2, **(c)** Model 3, **(d)** Model 5, **(e)** Model 6, **(f)** Model 7, and **(g)** Model 8 (chosen by AICc) in relation to pre- (small dashed line) and post- (large dashed line) stocking average values. Model 4 (Null model) is not included.

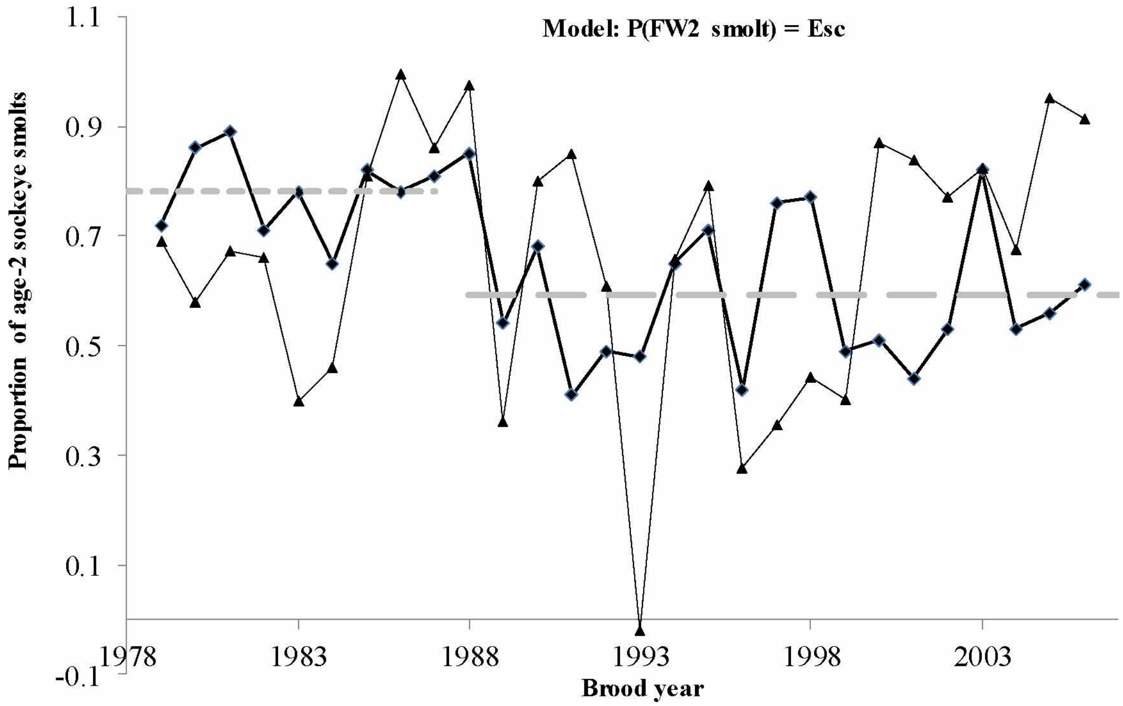


Residuals vs Fitted
Residuals
Predicted values
Normal Q-Q
Std. deviance resid.
Theoretical Quantiles
Scale-Location
√|Std. deviance resid.|
Predicted values
Residuals vs Leverage
Std. Pearson resid.
Cook's distance
Leverage

(a)

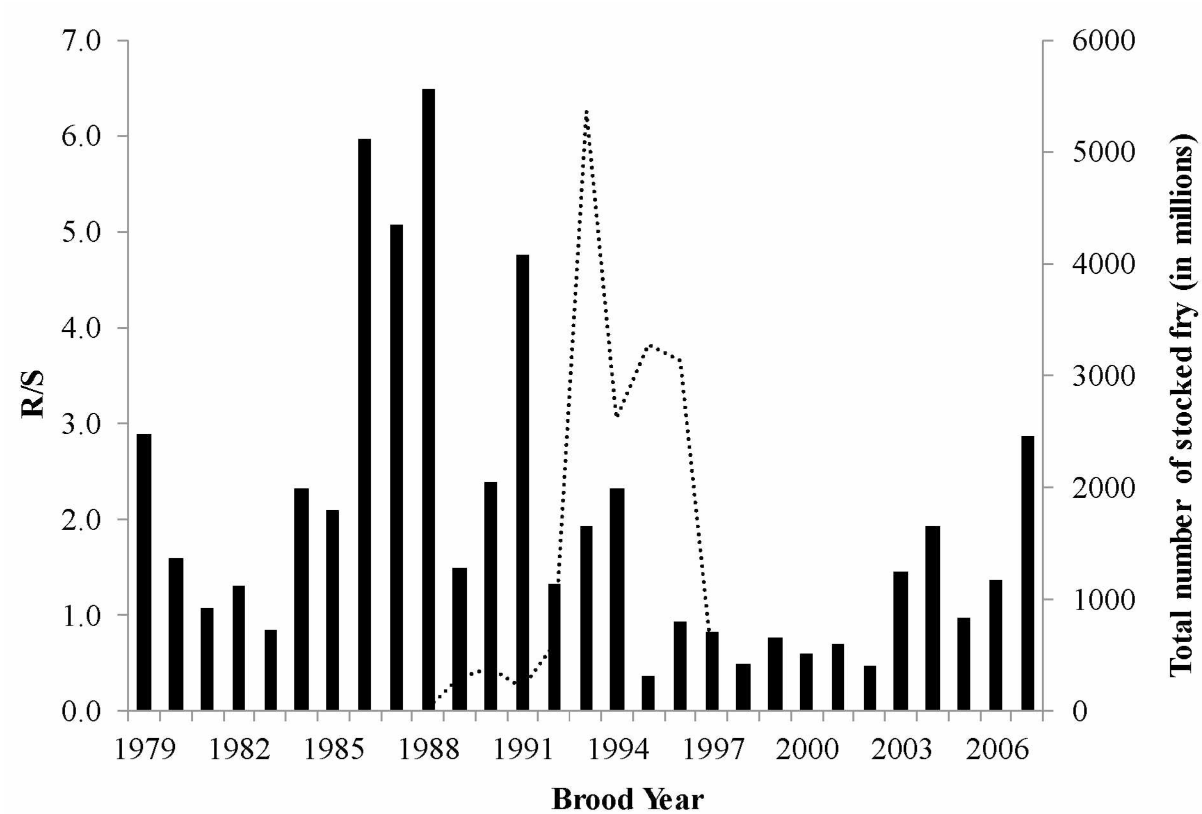


(b)
Appendix B-5. Model residuals **(a)** and autocorrelation plot **(b)** for the model explaining variation in the proportion of age-2 Chilkat Lake Sockeye Salmon smolts for brood years 1979-2006.



Appendix B-6. Observed (diamonds) versus predicted (triangles) values for the best model chosen to explain variation in the proportion of age-2 Chilkat Lake Sockeye Salmon smolts for brood years 1979-2006 in relation to pre- (small dashed line) and post- (large dashed line) stocking average values.

Appendix C



Appendix C-1. Recruits per spawner (black bars) for Chilkat Lake Sockeye Salmon for brood years 1979-2007 in relation to total number of stocked fry (dotted line).